

Estimation of Genetic, Environmental, and Competitional Variances in Standing Forests¹⁾

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Introduction

In 1963, SAKAI and HATAKEYAMA published a paper dealing with the method of estimating genetic parameters in standing forests of *Abies sochalinensis*. Further study on another species, *Cryptomeria japonica* D. DON, however, failed to yield reasonable estimates. This failure is considered to be due to intertree competition which may seriously interrupt an effective application of the method given at that time.

The present paper describes the result of a study on how to estimate genetic parameters in forests whose trees are competing with each other. This study has been financially supported by a grant from the Forestry Agency, Ministry of Agriculture and Forestry, Japan. Some of the data for the study have been provided by the courtesy of several prefectural forest-officers. Our thanks are due to all those who kindly helped the authors in their study.

Method of study

The method of study employed in the present paper is analogous to that of SAKAI and HATAKEYAMA (1963) with exception of the competitional variance component newly added to the formulas. The incorporation of competitional variance into the formulas was made in the following way. Let $V_{(\bar{x})}$ denote variance of average values of x trees grouped in clusters. It is assumed that, in addition to the genetic (G) and environmental (E) components, $V_{(\bar{x})}$ includes a competitional one (C). The general formula for $V_{(\bar{x})}$ is,

$$V_{(\bar{x})} = \frac{G}{x} + \frac{E}{x^b} + \frac{T_x C}{x} \dots \dots \dots (1)$$

$$\text{or } x V_{(\bar{x})} = G + x^B E + T_x C \dots \dots \dots (1')$$

where $B = 1 - b$. T_x , or the coefficient of competitional variance for clusters of x trees was obtained on the basis of the following premises: (1) Competition is effective between a given tree and those growing adjacently to it. (2) Competitive ability of individual trees is a character controlled by genes which are assumed to be genetically independent from genes controlling the character under investigation. (3) Competition between two trees benefits one of them and handicaps the other, but the gain obtained by the former is equal in absolute amount to the impairment endured by the latter (SAKAI 1955, p. 152). (4) Intensity of competitive effect is a function of intertree spacing; the effect increases rapidly as the spacing decreases (SAKAI 1955, p. 146, Fig. 12). (5) Effects of competition, plus or minus, on a given tree caused by trees growing around it are additive (SAKAI 1955, p. 152).

Let us now consider an arrangement of trees in a forest as given in Figure 1. If trees are planted in squares, a given tree, for instance tree 22 competes against eight trees around it, that is trees 11, 12, 13, 21, 23, 31, 32 and 33. Then the competitive effect tree 22 suffers from the eight competitors is

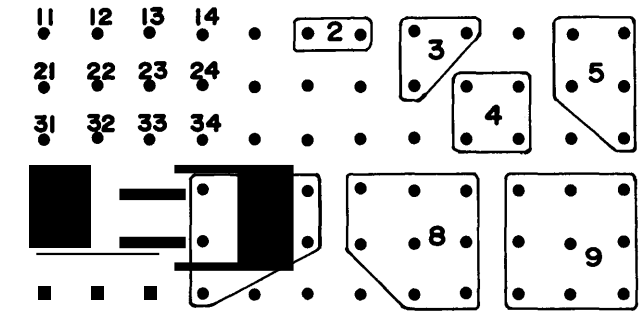


Figure 1. — Arrangement of trees, computation of competitive effect, and method of grouping two to nine trees.

as follows: Let the competitive ability of tree 22 be c_{22} and let the sum of competitive effects on it be a_{22} , then,

$$a_{22} = (c_{22} - c_{12}) + (c_{22} - c_{21}) + (c_{22} - c_{32}) + (c_{22} - c_{23}) + (c_{22} - c_{13}) + (c_{22} - c_{11}) + (c_{22} - c_{31}) + (c_{22} - c_{33}).$$

The distance between tree 22 and each of trees 11, 31, 13 and 33 is larger than that between tree 22 and any of trees 12, 21, 32 and 23, the ratio being $\sqrt{2} : 1 = 1.414 : 1$. Since from the premise (4), effect of competition between tree 22 and tree 11, 31, 13 or 33 is considered to be considerably weaker than that between tree 22 and tree 12, 21, 32 or 23, we may be not too wrong to assume that their effects are negligible. Then,

$$a_{22} = (c_{22} - c_{12}) + (c_{22} - c_{21}) + (c_{22} - c_{32}) + (c_{22} - c_{23}).$$

The competitional variance, C, is expressed by

$$C = E (a_{ij} - \bar{a}_{ij})^2 \dots \dots \dots (2)$$

The premise (3) tells that $a_{..} = \bar{a} = 0$, thus,

$$C = E (a_{ij}^2) \dots \dots \dots (3)$$

Then, a_{ij}^2 for the tree 22 is

$$a_{22}^2 = (4c_{22} - c_{12} - c_{21} - c_{32} - c_{23})^2 = 16c_{22}^2 + c_{12}^2 + c_{21}^2 + c_{32}^2 + c_{23}^2 \pm \text{all products}.$$

Since trees in a forest are expected to be distributed at random for genes of competitive ability, all products in the above equation equal to zero, and thus the expectation for the competitional variance on a single tree basis becomes

$$C = E (a_{ij}^2) = 20 c^2 = t_1 c^2 \dots \dots \dots (4)$$

The competitive effect on two adjoining trees, 22 and 23, is

$$a_{22} = 4c_{22} - c_{12} - c_{21} - c_{32} - c_{23} \\ a_{23} = 4c_{23} - c_{13} - c_{22} - c_{33} - c_{24}$$

Therefore,

$$a_{22} + a_{23} = 3c_{22} + 3c_{23} - c_{12} - c_{21} - c_{32} - c_{13} - c_{33} - c_{24}$$

and accordingly,

$$C_{(2)} = \frac{1}{4} E (a_{ij} + a_{i, j+1})^2 = 6 c^2 \dots \dots \dots (5)$$

Since $V_{(\bar{x})}$ in simultaneous equations is multiplied by x as seen in the equation (1'), the coefficient of $C_{(\bar{x})}$ should also be multiplied by x . Thus,

$$2C_{(2)} = 12c^2 = t_2 c^2 \dots \dots \dots (6)$$

In a similar way, coefficient of c^2 or t_x can be obtained for any number of trees of a cluster. The T_x , which is the re-

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Table 1. — Coefficients of competitiveness for $x = 1 - 9$

Cluster size, x	t_x	T_x
1	20	1.000
2	12	0.600
3	10.7	0.535
4	6.0	0.300
5	6.8	0.340
6	4.7	0.235
7	5.4	0.270
8	4.3	0.215
9	3.56	0.178

calculated coefficient regarding t_1 as unity for up to $x = 9$ is given in Table 1.

It is necessary to observe at clustering the following rules:

(1) Clustering should be made to have the trees arranged as shown in Figure 1 when four or more trees are grouped.

(2) Extremely poor trees or damaged ones which are apparently different from the majority of trees of the population should be discarded from the arrangement.

(3) The number of clusters decreases as the number of trees in each cluster increases. It is recommended in such a case to increase the number of degrees of freedom by pooling the mean squares obtained from repeated sampling and clustering.

The set of simultaneous equations for cluster size of 1 to 8 is presented below:

$$\begin{aligned}
 V_{(1)} &= G + E + C \\
 2 V_{(2)} &= G + 2^B E + 0.600 C \\
 3 V_{(3)} &= G + 3^B E + 0.535 C \\
 4 V_{(4)} &= G + 4^B E + 0.300 C \\
 5 V_{(5)} &= G + 5^B E + 0.340 C \\
 6 V_{(6)} &= G + 6^B E + 0.235 C \\
 7 V_{(7)} &= G + 7^B E + 0.270 C \\
 8 V_{(8)} &= G + 8^B E + 0.215 C
 \end{aligned} \quad \dots \dots (7)$$

G , E and C in the equations stand for genetic, environmental and competitiveness variances, respectively, and $B = 1 - b$, in which b is a constant lying between zero and unity.

Measuring $V_{(x)}$ from the data, various values between 0 and 1 are assigned to B , and the simultaneous equations are repeatedly solved by the method of the least squares in order to yield estimates of G , E and C for different B values. Observed mean squares and expected variances computed on the basis of estimated G , E and C are compared, and B_0 , G_0 , E_0 and C_0 which show the best fit are determined.

The standard errors of estimated components are obtained by the inverse matrix (for details, consult GOULDEN 1952).

$$S.E._{(G_0)} = \sigma_0 \sqrt{c_{11}}$$

$$S.E._{(E_0)} = \sigma_0 \sqrt{c_{22}}$$

$$S.E._{(C_0)} = \sigma_0 \sqrt{c_{33}}$$

where $\sigma_0 = \frac{(R.S.S.)_0}{n-4}$ in which $(R.S.S.)_0$ is the corresponding minimum residual sum of squares and c_{11} , c_{22} and c_{33} are diagonal elements of the inverse matrix. n is the number of comparisons.

The heritability is obtained from

$$h^2 = \frac{G_0}{G_0 + E_0 + C_0} \dots \dots (8)$$

In order to find genetic, environmental and competitiveness correlations between two characters, the partition into components of covariance is performed which has the same form as the simultaneous equations (7) with components of covariance in place of the components of variance.

$$x W_{(x)}(PQ) = W_{G(PQ)} + x^B W_{E(PQ)} + T_x W_{C(PQ)} \quad (9)$$

where $W_{(x)}(PQ)$ stands for covariance between mean values of P and Q characters in clusters of x trees. $W_{G(PQ)}$, $W_{E(PQ)}$ and $W_{C(PQ)}$ are genetic, environmental and competitiveness components of covariance between P and Q characters whose standard errors are computed in the same way as above mentioned. Genetic, environmental and competitiveness correlations, i. e. $r_{G(PQ)}$, $r_{E(PQ)}$ and $r_{C(PQ)}$ are obtained in the following way:

$$\begin{aligned}
 r_{G(PQ)} &= \frac{W_{G_0(PQ)}}{\sqrt{G_{0(P)} \times G_{0(Q)}}} \\
 r_{E(PQ)} &= \frac{W_{E_0(PQ)}}{\sqrt{E_{0(P)} \times E_{0(Q)}}} \\
 r_{C(PQ)} &= \frac{W_{C_0(PQ)}}{\sqrt{C_{0(P)} \times C_{0(Q)}}}
 \end{aligned} \quad (10)$$

Materials for the study

Materials for the present study are artificially planted forests of *Cryptomeria japonica* D. DON, grown in several districts of Japan. Number of trees contained in each for-

Table 2. — Genetic, environmental, and competitiveness variance components of stem diameter at breast height and tree height in *Cryptomeria*

Forest	b_0	G_0	E_0	C_0	h^2
Stem diameter or girth at breast height					
Clone (Kumotoshi)	0.09 (0.12)*	1.0559 ± 5.372	29.4552 ± 0.935 (31.4200 ± 1.008)*	1.2855 ± 5.094	—
Otobe (Hokkaido)	0.16	3.4834 ± 1.795	4.1730 ± 0.299	18.8301 ± 1.847	0.132
Yakumo (Hokkaido)	0.08	4.7154 ± 0.809	3.9110 ± 0.114	4.6169 ± 0.862	0.356
Hayaguchi (Akita)	0.41	10.7282 ± 5.487	12.0804 ± 1.507	25.7858 ± 4.690	0.221
Tree height					
Clone (Kumotoshi)	0.15 (0.11)*	0.2982 ± 3.635	1.2766 ± 0.704 (1.2457 ± 1.052)*	—0.3411 ± 3.343	—
Yakumo (Hokkaido)	0.17	0.7563 ± 2.148	1.6638 ± 0.365	0.5675 ± 2.197	0.253
Hayaguchi (Akita)	0.43	4.4032 ± 1.057	4.5071 ± 0.302	2.6123 ± 0.886	0.382

*) Figures in the parentheses stand for the estimation obtained from the equation, $V_{(x)} = \frac{E}{x^b}$.

est varied from 100 to more than 200. Trees in the same forest were of the same age, about 20 years old in some forests and about 30 in others. Choice among forests was made for lesser number of missing trees and higher uniformity of intertree spacing. As a matter of fact, a certain number of trees are naturally or accidentally missing in every forest owing either to natural death at an early age or artificial thinning. To all trees of a forest were assigned numbers in running order and they were individually mapped on a section paper. Each tree was measured for tree height and stem diameter at breast height.

Results of the study

The estimated values of b_0 , G_0 , E_0 and C_0 for one clone and three seed-propagated forests, together with heritability values are presented in Table 2.

Examination of estimated values in the clone forest in Table 2 reveals that G_0 value for stem diameter was 1.0559 ± 5.372 , i.e. G_0 is interpreted as to be almost zero. This is quite reasonable because the whole forest belonged to a clone involving no genetic variation. The same has been again found for tree height, the G_0 value being 0.2982 ± 3.635 . It is interesting that the competitive variance, C_0 , in the clone forest can also be regarded as zero; it was 1.2855 ± 5.094 for stem diameter and -0.3411 ± 3.343 for tree height. Table 2 also presents two estimates of environmental variance in the clone forest. One of them found in parentheses was obtained by solving the equation,

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

which is based on the assumption that the variance in a clone is solely environmental. It is found that the two estimates proved to be approximately the same.

In the three seed-propagated forests, the estimated values of b_0 , G_0 , E_0 and C_0 were variable. It is a noteworthy fact that the competitive variance of stem diameter is large in comparison with its genetic or environmental variance, whereas as to tree height, it is rather small. The heritability values of stem diameter, consequently, were as low as 0.132 to 0.356, although the similarly low heritability also holds for tree height.

The comparison between the observed mean squares and the theoretical variances is found in Figure 2.

The solid lines represent the observed values while the white circles demark the expected ones. It is found from Figure 2 that the agreement is satisfactory.

Genetic, environmental and competitive correlations between stem diameter and tree height are presented in Table 3.

Environmental correlations are always high being $0.764 \approx 0.968$, while genetic correlations are between $0.645 \approx 0.992$. Competitive correlations are a little lower than others, the values being $0.64 \approx 0.65$.

Discussion

As mentioned in the introduction, SAKAI and HATAKEYAMA (1963) succeeded in estimating the genetic parameters in *Abies* without taking into account the effect of intertree

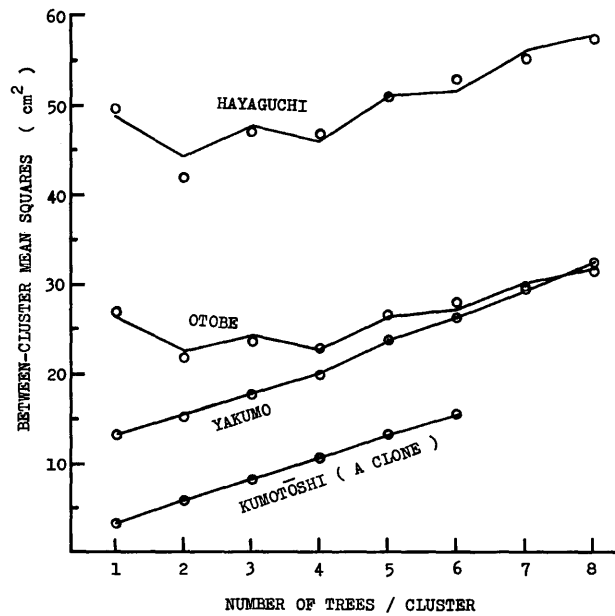


Figure 2. — Observed and calculated between-cluster mean squares of stem diameter at breast height in *Cryptomeria japonica* D. Don. Circles demark the calculated values.

competition. The same method, however, was found to be not useful for *Cryptomeria*. The possible reason for this is the occurrence of intertree competition which upsets the effect of environmental heterogeneity. It is theoretically expected that environmental heterogeneity may cause trees growing in close vicinity to show similar growth in comparison with those growing apart, whereas intertree competition makes them dissimilar by favouring one and dis-favouring the other. As to the particular study on intertree competition by the use of correlation coefficients between adjoining trees, we expect a separate paper to follow this one before long.

Consideration on intertree competition led the writers to construct a set of simultaneous equations which involve competition contribution in addition to genetic and environmental ones. Partition of those three variance components by solving those equations for a few *Cryptomeria* forests gave the following results: In the clone forest, the genetic as well as the competitive variance was found to be almost nil: the genetic variance for stem diameter and tree height was 1.0559 ± 5.372 and 0.2982 ± 3.635 , and the competitive variance was 1.2855 ± 5.094 and -0.3411 ± 3.343 , respectively. That the genetic variance in a clone is zero meets our expectations, but as to competitive variance nothing indicates that trees of the same genotype do not compete with each other.

In order to test the accuracy of the estimated amount of environmental variance in the clone forest, an attempt was made to solve simultaneously B and E by using $x V_{(\bar{x})} = x^B E$ or $\log(x V_{(\bar{x})}) = B \log x + \log E$, on the assumption that variation in a clone forest is solely environmental. The results are given in Table 2 in asterisked pa-

Table 3. — Genetic, environmental, and competitive covariance components between stem diameter at breast height (D) and tree height (H) in *Cryptomeria*.

Forest	b_0	$W_{G(D H)}$	$W_{E(D H)}$	$W_{C(D H)}$	$r_{G(D H)}$	$r_{E(D H)}$	$r_{C(D H)}$
Clone (Kumotoshi)	0.08	0	4.7793 ± 1.054	0	0	0.764	0
Yakumo (Hokkaido)	0.15	1.2188 ± 0.866	2.1478 ± 0.152	1.0428 ± 0.849	0.645	0.842	0.644
Hayaguchi (Akita)	0.62	6.8226 ± 2.385	7.1415 ± 1.036	5.3173 ± 1.537	0.992	0.968	0.648

rentheses. It is found from the table that thus estimated b , i. e. $1 - B$, and E are not much different from b_0 and E_0 .

In seed-propagated forests, G and C values were statistically significant at least for stem diameter. For tree height, G and C values happened to be almost zero in the Yakumo forest. That this forest is not a clone was already indicated by the statistically significant values of G and C for stem diameter.

Competitional variance tended to be larger than genetic or environmental variance for stem diameter, but smaller for tree height. This indicates that stem diameter is more susceptible to competition than tree height.

Heritability values were computed and are represented in the sixth column of Table 2. They are generally very low. Reference is made in connection with the present results to the results of studies in *Cryptomeria japonica* conducted by TODA (1957, 1959 and 1961). He found that the heritability of tree height and stem girth in *Cryptomeria japonica* was $0.68 \approx 0.89$ and $0.58 \approx 0.84$, respectively, when it was estimated by the comparison between a seed-propagated population and a clone. It was, however, as low as 0.265 for tree height and 0.260 for stem girth when estimated by the method of family analysis in a breeding experiment. The values obtained from the family analysis were very close to ours either for stem diameter or tree height, whereas the heritability estimated by a comparison between a seed-propagated and a clone forest was very high probably because the genetic variance in the latter involved the effect of competition or competition variance in addition to the genuine genetic variance.

Stem diameter and tree height are positively and highly correlated genetically as well as environmentally. They are also positively correlated competitionally. Recollecting the fact that stem diameter is more susceptible to competition than tree height as mentioned above, it is possible that in the first place the former is influenced by competition accompanied by correlated changes in the latter.

The very low heritability values of tree height and stem diameter in *Cryptomeria japonica* D. DON indicate that the selection of elite-trees in forests of this species would be difficult. It is accordingly important to investigate how to select genotypically superior trees in face of intraforest competition in such a species as *Cryptomeria japonica*.

Conclusion

If intertree competition occurs in a forest, it acts toward cancelling out the effect of environment, whereby the method of estimating genetic parameters as worked out by SAKAI and HATAKEYAMA (1963) becomes useless. In order to find out the genetic variance components in a forest whose trees are competing with each other, it is necessary to solve a set of simultaneous equations for mean squares between clusters including a various number of trees. The simul-

taneous equations include the expected components of genetic, environmental and competition variances.

It was found from the computation that in the clone, not only genetic variance but also competition variance was zero, i. e. trees in a clone are isogenic and they do not compete with each other. In seed-propagated forests, however, competition variance proved to be considerably large in some forests. The heritability was estimated for stem diameter and tree height, both being approximately 0.2 or 0.3. These low values of heritability indicate that the selection of elite-trees in *Cryptomeria* forests would be difficult.

Genotypic, environmental and competition correlations were estimated in a similar way as above described. It was found from this analysis that environmental correlation between stem diameter and tree height was as high as $0.76 \approx 0.96$, whereas the competition correlation was about 0.64. Genetic correlation between them was 0.645 in one case, but 0.992 in another. It is concluded that stem diameter is more susceptible to competition than tree height, and the initial influence of competition on stem diameter induces secondary effects on tree height by competition correlation.

Summary

This paper describes results of an investigation on how to estimate genetic parameters in standing forests of *Cryptomeria japonica* D. DON by partitioning the phenotypic variance or covariance into genetic, environmental and competition components. It was found that in a clone forest, trees did not compete with each other, whereas those in a seed-propagated forest competed intensely or weakly. Intertree competition affects severely stem diameter but to a lesser degree tree height. Heritability values for stem diameter at breast height and tree height in *Cryptomeria* were very low, but the genetic correlation between them was positive and high. These results indicate that an effective selection of genetically superior trees in *Cryptomeria* forests would be difficult.

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