

The Heritability of Tree Height and Stem Girth in *Cryptomeria* through Sexual Reproduction¹⁾

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Introduction

Within a population of forest trees, a large amount of variation is generally observed in their growth or other characteristics and the problem has always been how much of this variation is determined by environmental factors and how much by the inherent nature of the trees. This problem can be solved by using the concept of "heritability". Briefly, heritability is the relative amount of heritable variance in the total variance of the population. It serves as a basis for estimating the effects of selection or for determining the best method of selection, and has become a remarkably useful tool for use in forest tree breeding.

In a previous paper, one of the authors (TODA, 1957) roughly estimated the heritability of several quantitative characters in a *Cryptomeria* stand by comparing the variation in a 42 year old stand grown from seed with that in another stand of almost the same age but consisting of trees of a genetically more simple population produced by repeated vegetative propagation. These estimations were of heritability in the broad sense based on the total genetic variance, and they cannot be applied when sexual reproduction is employed, where heritability in the narrow sense, based upon the additive genetic variance, must be used. The author could not use this material for estimating the heritability in the narrow sense, and this aspect of heritability was merely discussed reference being made to rough estimates derived from simple data obtained from a Scots pine progeny trial in Germany.

In *Cryptomeria* selected phenotypic elite trees are generally propagated by cuttings and are planted as mixtures of clones, so the effect of selection may be fairly estimated from heritability in the broad sense. Heritability in the narrow sense appears, therefore, to be of little use in the breeding of this species. But we often find selected trees which are very difficult to root; also rooted cuttings from old parent trees may not fully display their inherent nature in their growth habit, and it may be necessary to utilize the material in a seed orchard. Even if we assume that seed orchards are not necessary, it is evident that we need a considerable number of seedlings from elite material for the purpose of repeated selection, and it is then desirable to know something about the growth of these seedlings. Also from the theoretical point of view, it is necessary to determine heritability in the narrow sense as well as that in the broad sense in order to examine the genetic behaviour of a population.

At present, it is very difficult to find in Japan suitable material for the estimation of heritability, but, fortunately, a trial of single mother trees in the Tiba Forest of Tokyo University seemed considerably suitable for this purpose. Although this is not completely satisfactory, the results of the calculations are reported here as an example

¹⁾ The Japanese text of the same contents is in the press in Bull. Gov't Forest Exp. Sta. No. 112.

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of the estimation of heritability of tree height and stem girth.

The present paper is the result of calculations by TODA from the measurements of SATOO and others (1952) in the trial plantations established by NAKAMURA and others (1937).

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Material and Methods

Three reports in Japanese and a summary in German (1956) on this trial have already been published, so it is not necessary to describe it in detail. We will only mention here, that the two experimental plantations at Hino-kinudai and Sakuragao in the Tiba University Forest were planted in the spring of 1934 with seedlings which had been sown in the spring of 1931. In these plantations, individual trees from each mother tree have been grown in a thorough mixture. Measurements were made in April 1951. The data has been analysed once and discussed in the third report (1952) and in the German summary (1956). In the third report, a comparison was made between the progenies of ten mother trees from three mother stands, Myookan'yama, Sakuragao and Kazisaka. As far as can be judged from the results, the Kazisaka group of mother trees belongs to a different genetic population from the other two, which are apparently almost the same in their genetic nature. So, for the present analysis the material consists of the progenies of six mother trees, three each from the Myookan'yama and Sakuragao groups.

Tree height was measured with a cloth tape and bamboo pole to the nearest 0.1 meter, and diameter at breast height was measured in two directions with calipers to the nearest 0.1 centimeter.

From the data thus obtained, it is found that the macroscopic variation of the site conditions has had a remarkable effect upon the measurements. The arrangement of the individuals measured is shown in Figure 1, which shows the irregular mixture of the progenies. There is no easy method of eliminating the effects of the macroscopic variation in site conditions. We have, therefore, divided the plantations into plots by means of rows and columns ten meters wide. We have assumed that the two plantations each reflect the average site effects, that the effects of the plots are additively determined by the effects of rows and columns and that the progeny from a single mother tree shows a certain total value in accordance with the genetic nature of the mother tree. Thus, the measurement of an individual tree can be represented by the mathematical model:

$$x_{ind.} = \mu + \tau_i + \pi_j + \rho_{jk} + \gamma_{jl} + e_{ind.}$$

where,

- μ : general mean,
- τ_i : deviation by mother tree,
- π_j : deviation by plantation,
- ρ_{jk} : deviation by row from the plantation mean,
- γ_{jl} : deviation by column from the plantation mean,
- $e_{ind.}$: residual deviation of each individual.

Table 1 (b). — The Number and Sum of the Measurements (Height and Diameter at Breast Height) by Plots, Sakuragao Plantation and Grand Total.

		Column																		Grand Total					
		10			11			12			13			14			15			Total			Grand Total		
		No.	H.	D.	No.	H.	D.	No.	H.	D.	No.	H.	D.	No.	H.	D.	No.	H.	D.	No.	H.	D.	No.	H.	D.
7	A	1	3.5	3.7	—	—	—	2	13.6	17.4	—	—	—	—	—	—	—	—	—	3	17.1	21.1	—	—	—
	B	3	24.6	34.2	1	9.3	13.5	—	—	—	—	—	—	—	—	—	—	—	—	2	49.2	68.0	—	—	—
	C	—	—	—	1	4.6	5.8	—	—	—	—	—	—	—	—	—	—	—	—	2	11.4	16.5	—	—	—
	D	1	8.6	13.8	5	23.7	33.7	7	43.3	59.8	—	—	—	—	—	—	—	—	—	13	75.6	107.3	—	—	—
	E	1	6.9	9.2	1	6.7	10.6	—	—	—	—	—	—	—	—	—	—	—	—	3	20.6	30.5	—	—	—
	F	6	43.6	60.9	10	50.3	70.4	11	73.0	101.4	—	—	—	—	—	—	—	—	—	28	173.9	243.4	—	—	—
	Total	—	—	—	2	15.7	19.3	4	34.8	46.1	1	9.9	14.3	1	8.6	10.6	—	—	—	9	78.7	104.6	—	—	—
8	A	3	20.3	28.5	1	10.0	15.8	2	15.5	18.1	1	9.2	12.2	2	15.3	19.2	—	—	—	9	70.3	93.8	—	—	—
	B	—	—	—	2	16.1	22.0	1	9.7	11.2	1	12.8	23.0	4	38.6	56.2	—	—	—	9	70.3	93.8	—	—	—
	C	—	—	—	1	7.8	11.8	—	—	—	—	—	—	—	—	—	—	—	—	4	38.6	56.2	—	—	—
	D	1	6.8	9.8	3	28.6	40.0	1	7.8	11.8	2	16.4	20.0	3	19.5	21.5	—	—	—	10	79.1	103.1	—	—	—
	E	2	11.1	16.9	5	43.3	62.9	2	14.9	21.0	—	—	—	1	8.4	10.7	—	—	—	10	79.1	103.1	—	—	—
	F	—	—	—	2	14.9	21.0	—	—	—	—	—	—	1	6.2	6.2	1	4.9	6.2	2	11.1	12.4	—	—	—
	Total	6	38.2	55.2	10	91.6	133.0	7	54.5	74.1	7	60.0	75.4	7	62.9	86.4	7	48.3	57.5	44	355.5	481.6	—	—	—
9	A	—	—	—	1	11.7	17.4	—	—	—	—	—	1	12.3	18.6	2	16.5	20.6	—	4	40.5	56.6	—	—	—
	B	4	24.2	34.4	2	16.5	21.9	4	44.5	59.7	2	24.0	27.3	—	—	—	—	—	—	12	109.2	143.3	—	—	—
	C	—	—	—	1	12.3	16.6	2	22.6	31.3	3	36.3	48.6	—	—	—	—	—	—	6	71.2	96.5	—	—	—
	D	1	5.0	6.3	—	—	—	—	—	—	—	—	—	1	8.0	10.0	—	—	—	2	13.0	16.3	—	—	—
	E	2	18.2	28.8	2	22.5	31.5	2	24.0	33.4	—	—	—	—	—	—	—	—	—	2	46.7	64.7	—	—	—
	F	2	14.9	24.7	2	21.0	32.7	—	—	—	—	—	—	1	7.0	9.2	7	71.7	102.9	6	57.1	83.8	—	—	—
	Total	9	62.3	94.2	8	84.0	120.1	8	91.1	124.4	8	91.1	124.4	7	83.4	109.3	5	41.9	51.4	37	362.7	499.4	—	—	—
10	A	—	—	—	1	9.8	14.0	3	28.6	37.0	—	—	—	—	—	—	—	—	—	6	53.1	72.2	—	—	—
	B	1	7.4	9.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	7.4	9.7	—	—	—
	C	1	9.4	15.4	—	—	—	—	—	—	—	—	—	1	12.3	15.4	2	14.1	21.3	7	68.6	94.7	—	—	—
	D	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	E	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	F	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Total	3	26.6	39.1	3	26.6	39.1	6	61.4	79.6	1	12.3	15.4	4	28.8	42.5	14	129.1	176.6	14	129.1	176.6	—	—	—
Total	A	1	9.7	14.3	4	37.2	50.7	7	63.4	83.1	2	22.2	32.9	5	39.8	52.4	19	172.3	233.4	72	562.4	787.9	—	—	—
	B	3	20.3	28.5	3	23.9	31.6	8	73.6	95.2	3	33.2	39.5	2	15.3	19.2	25	204.0	267.9	64	465.3	623.2	—	—	—
	C	—	—	—	7	53.1	74.3	7	74.4	98.6	5	61.4	87.0	2	14.1	21.3	24	227.6	315.4	51	432.9	610.5	—	—	—
	D	1	6.8	9.8	2	12.4	17.6	1	6.8	10.7	2	16.4	20.0	4	27.5	31.5	14	103.5	135.9	31	218.0	291.2	—	—	—
	E	2	11.1	16.9	8	70.1	105.5	9	61.1	86.2	1	8.4	10.7	1	7.0	9.2	30	225.0	321.7	61	464.3	674.3	—	—	—
	F	—	—	—	3	27.7	43.3	—	—	—	—	—	—	2	15.3	17.8	11	88.8	126.7	15	129.0	185.5	—	—	—
	Total	6	38.2	55.2	25	197.5	288.1	28	215.4	303.7	32	285.5	380.8	16	165.6	221.8	16	119.0	151.4	123	1021.2	1401.0	294	2271.9	3172.6

Table 2. — Examples of Normal Equations. Derivatives of Mother Tree Factors.

		Unknowns															Constants																				
		m	t _A	t _B	t _C	t _D	t _E	t _F	P ₁	P ₂	r ₁	r ₂	r ₃	r ₄	r ₅	r ₆	r ₇	r ₈	r ₉	r ₁₀	c ₁	c ₂	c ₃	c ₄	c ₅	c ₆	c ₇	c ₈	c ₉	c ₁₀	c ₁₁	c ₁₂	c ₁₃	c ₁₄	c ₁₅	H.	D.
Coefficients	72	72	0	0	0	0	0	53	19	11	11	14	7	6	4	0	9	4	6	2	4	1	3	7	2	10	11	13	0	1	4	7	2	5	562.4	787.9	
	64	0	64	0	0	0	39	25	7	10	4	11	6	1	3	9	12	1	1	5	12	3	1	8	6	1	2	3	6	3	8	3	2	465.3	623.2		
	51	0	0	51	0	0	27	24	4	6	7	7	2	1	7	4	6	7	0	0	6	3	8	0	0	3	7	0	3	7	7	5	2	432.9	610.5		
	31	0	0	0	31	0	0	17	14	1	10	1	10	1	2	1	2	2	10	2	0	0	1	3	0	2	0	1	10	1	4	2	1	2	218.0	291.2	
	61	0	0	0	0	61	0	31	30	4	6	8	7	6	0	13	10	7	0	0	5	4	2	2	2	1	3	7	7	2	8	9	9	1	464.3	674.3	
15	0	0	0	0	0	15	4	11	0	2	1	1	0	0	3	2	6	0	0	0	0	0	2	0	1	0	1	0	0	3	0	3	2	129.0	185.5		

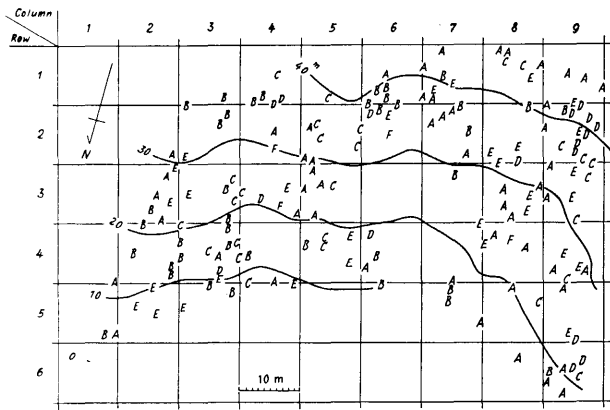


Fig. 1 (a). — Distribution of the trees measured. These were derived from six mother trees. Hinokinodai plantation.

The estimates of the parameters in the model can be obtained by the method of least squares.

The values, where the measurements have been adjusted for the estimates of the parameters for site quality, represent the expectations of the individual growths on the ideal site of average quality. And we can then calculate the mother tree fraction of the net variance of the population from them. For ease of computation, the mean squares for individuals and for mother trees were calculated separately, adjusting the measurements not only for site quality but also for the mother tree effects at the same time.

On the other hand, a mixed population consisting of the progenies of many mother trees taken at random in a natural population shows almost the same genetic nature as that of the mother population. So the residual net variance of the population excluding the influence of macroscopic environmental variation is represented by the formula:

$$\sigma_P^2 = \sigma_g^2 + \sigma_d^2 + \sigma_i^2 + \sigma_e^2 + \sigma_j^2$$

where:

- σ_g^2 : additive genetic variance,
- σ_d^2 : non-additive genetic variance due to dominance,
- σ_i^2 : non-additive genetic variance due to epistasis,
- σ_e^2 : variance proportional to the environmental variation,
- σ_j^2 : variance due to non-proportional interactions between genotypes and environments,

and the mother tree fraction of the variance is represented by

$$\sigma_m^2 = 1/4 \sigma_g^2$$

which is easily verified in a F_2 population model. So we can easily estimate the heritability in the narrow sense by the formula:

$$h^2 = \frac{\sigma_g^2}{\sigma_P^2} = \frac{4 \sigma_m^2}{\sigma_P^2}$$

The Calculations

1. The estimation of site and mother-tree quality

The number of individuals and the sum of the measurements are shown in Table 1 plot by plot.

According to the assumed model, we chose the estimates of parameters (μ , τ_i , π_j , ρ_{jk} , γ_{jl}), as m , t_i ($i = A, \dots, F$), p_j ($j = 1, 2$), r_{jk} ($jk = 1, \dots, 6; 7, \dots, 10$) and c_{jl} ($jl = 1, \dots, 9; 10, \dots, 15$), respectively. The numerical value of

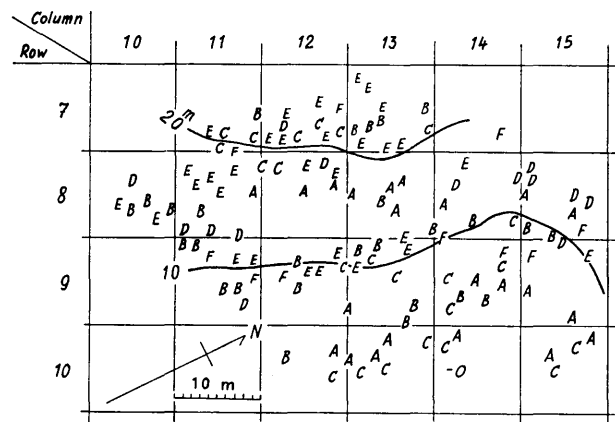


Fig. 1 (b). — Distribution of the trees measured. These were derived from six mother trees. Sakuragao plantation.

these estimates were determined so as to minimize the following over-all sum:

$$\sum (x_{\text{ind.}} - m - t_i - p_j - r_{jk} - c_{jl})^2 = \sum e_{\text{ind.}}^2$$

It is sufficient to solve the following normal equations, which were obtained by differentiating the sum of squares with respect to each unknown in turn and set the derivatives equal to zero,

$$\sum (m + t_i + p_j + r_{jk} + c_{jl}) = \sum x_{\text{ind.}}$$

where the sum is taken over all measurements whose equations contain the parameter to be estimated. For example, equations derived from mother tree factors are shown in Table 2. As there are thirty four unknowns, the number of normal equations obtained is also thirty four, but in the solving of the equations, six equations disappear by becoming zero on both sides. We can now supply the following six equations according to the assumptions in the model:

$$\begin{aligned} 72t_A + 64t_B + 51t_C + 31t_D + 61t_E + 15t_F &= 0 \\ 171p_1 + 123p_2 &= 0. \\ 27r_1 + 45r_2 + 35r_3 + 35r_4 + 21r_5 + 8r_6 &= 0. \\ 28r_7 + 44r_8 + 37r_9 + 14r_{10} &= 0. \\ 3c_1 + 14c_2 + 24c_3 + 16c_4 + 18c_5 + 16c_6 + 19c_7 &+ 24c_8 + 39c_9 = 0. \\ 6c_{10} + 25c_{11} + 28c_{12} + 32c_{13} + 16c_{14} + 16c_{15} &= 0. \end{aligned}$$

From these equations we obtain the estimates of parameters, which are shown in the Table 3. For the purpose of minimizing the accumulation of error, the estimates were determined to three decimal places.

2. The estimation of heritability

We have estimated the mother tree fraction of the variance by the method of analysis of variance. However, the sum of squares for plantations, rows and columns do not satisfy the addition theorem, because the arrangement of the material is extremely disproportionate. So, it is no use determining them, and we are better to compute the sum of squares for individuals from the values adjusted for site quality and mother trees and that for mother trees from t_i . Namely, sum of squares for individuals:

$$\sum (m + e_{\text{ind.}})^2 - \frac{[\sum (m + e_{\text{ind.}})]^2}{N} = \sum e_{\text{ind.}}^2$$

and sum of squares for mother trees:

$$\sum k_i t_i$$

where, N : grand total of individuals = 294,

k_i : number of trees for each mother tree.

Table 3. — Estimations of General Mean, Deviations by Mother Trees and by Site Conditions.

	H.	D.		H.	D.	
mean	7.728	10.791	Hinokinodai plantation			
deviations by mother trees			plantation	p ₁	0.391	-0.372
t _A	+0.071	+0.120	rows	r ₁	-1.766	-2.244
t _B	-0.670	-1.356		r ₂	-0.261	-0.232
t _C	+0.786	+1.264		r ₃	+0.734	+0.445
t _D	-0.335	-0.919		r ₄	+0.973	+1.474
t _E	+0.053	+0.455		r ₅	+0.072	+0.280
t _F	+0.322	+0.961		r ₆	-0.229	-0.252
Sakuragao plantation			columns	c ₁	+2.200	+4.673
deviations by	plantation	p ₂	+0.543	+0.517		
	rows	r ₇	-2.443	-3.409		
		r ₈	+0.138	+0.070		
		r ₉	+1.467	+2.097		
		r ₁₀	+0.575	+1.056		
	columns	c ₁₀	-1.669	-1.499		
		c ₁₁	-0.306	+0.306		
		c ₁₂	-0.383	-0.345		
		c ₁₃	+0.962	+0.963		
		c ₁₄	+1.343	+1.504		
		c ₁₅	-1.493	-2.740		

Adjustment of measurements was made to two decimal places.

The total number of degrees of freedom (294 - 1 = 293) is reduced by that for plantations (2 - 1 = 1), for rows (10 - 2 = 8) and for columns (15 - 2 = 13), and then the residue is divided into two, one for mother trees (6 - 1 = 5) and the other for individuals (293 - 1 - 8 - 13 - 5 = 266).

The tables of analysis of variance for tree height and stem diameter (Tables 4 and 5) were obtained by these calculations. Here, total mean squares becomes an estimate for the net variance of the population excluding the influences of macroscopic variation of environment, and the mean squares for mother trees and individuals, on the other hand, become the estimates of

$$k_o \sigma_m^2 + \sigma_o^2 = 1/4 k_o \sigma_g^2 + \sigma_o^2 \quad \text{and}$$

$$\sigma_o^2 = 3/4 \sigma_g^2 + \sigma_d^2 + \sigma_i^2 + \sigma_e^2 + \sigma_j^2$$

Table 4. — Analysis of Variance of Tree Height (The Macroscopic Environmental Variation is already eliminated).

Source of Variation	d. f.	Sum of Squares	Mean Square
Mother Trees	5	65.81	13.161
Individuals	266	809.17	3.042
Total	271	874.98	3.229

Table 5. — Analysis of Variance of Diameter at Breast Height (The Macroscopic Environmental Variation is already eliminated).

Source of Variation	d. f.	Sum of Squares	Mean Square
Mother Trees	5	252.86	50.572
Individuals	266	3156.02	11.865
Total	271	3408.88	12.579

respectively. In the above formula, k_o is the average number of trees in a progeny and is shown by the following formula:

$$k_o = \frac{1}{n-1} \left\{ \sum k - \frac{\sum k^2}{\sum k} \right\} = 47.38$$

where,

$$n = 6$$

$$\sum k = 294$$

$$\sum k^2 = 72^2 + 64^2 + 51^2 + 31^2 + 61^2 + 15^2 = 16788$$

Therefore, the estimate of the mother tree fraction of variance, 1/4 σ_g², is calculated by:

$$\frac{\text{m. s. for mothers} - \text{m. s. for individuals}}{k_o}$$

and, for tree height, it is calculated as

$$\frac{13.161 - 3.042}{47.38} = 0.214$$

and for diameter of stem, as

$$\frac{50.572 - 11.865}{47.38} = 0.817$$

So, the heritability of tree height is estimated as

$$\frac{0.214 \times 4}{3.229} = 0.265$$

and that of diameter of stem, as

$$\frac{0.817 \times 4}{12.579} = 0.260$$

Discussions

In the previous paper, TODA (1957) estimated the heritability of tree height in Scots pine as being about 24 per cent using simple data published in Germany which shows that the average standard deviation of progenies from

single mother trees is about three per cent smaller than that of the bulk population. Assuming that the heritability in the narrow sense in *Cryptomeria* is also of the same order as for Scots pine, TODA concluded that the expected effects of selection when the selected trees were utilized in seed orchards would be about one third of that obtained if cuttings from them were directly planted in the forest. This is because the heritability of tree height in the broad sense in *Cryptomeria* is nearly 70 per cent.

Now we have obtained estimates of heritability of tree height and stem girth in *Cryptomeria* itself, and both of them are quite similar to the estimate for Scots pine. Indeed, we cannot find differences among these three estimates because it is considered that the basis of calculation is not satisfactory for this purpose and the accuracy of the estimations is therefore doubtful. All the estimates appear to be ca. 25 per cent or nearly a quarter. Consequently, it is reasonable to consider at present that the effects of selection for tree height and stem girth in *Cryptomeria* when sexual reproduction is applied will be about one half or one third of that obtained with vegetative propagation.

The calculation of the expected effects of selection is not the only benefit to be obtained from estimating heritability. It also enables us an important insight into the genetic nature of the population. The fact that heritability in the narrow sense is one half or one third of that in the broad sense shows us that the additive genetic variance of the population, which is determined by the number of effective genes, is smaller than the non-additive portion of the genetic variance, which is determined by the effects of dominance or epistasis. Indeed, the latter may be twice as large as the former. So, we must pay attention to the effects of dominance or epistasis in the breeding of forest trees.

We do not know the proportion of dominance and epistasis within the non-additive genetic variation of the population, but it may be acceptable to assume that dominance occupies the greater part of the variation, and this suggests that the utilization of heterosis will produce a marked effect. It has often been stated that in forest tree breeding we must make use of hybrid vigour. The statement has hitherto been based on the observation of interspecific hybrids and so on, but we are now able to say that the examination of variation yields additional evidence for the truth of this statement. However, problems are still left including that how we are to organize a scheme of tree improvement to exploit heterosis when sexual reproduction is employed.

So far this discussion has been based on the two limited estimations of heritability one in the narrow sense and the other in the broad sense, but these values are not sufficiently concrete to permit of detailed discussions. First, we must recognize the fact that the materials employed in the estimation are not the same. Heritability in the broad sense has been estimated from a 42 year old stand in Miyazaki Prefecture and the original provenance of the seed is not known. Heritability in the narrow sense has, on the other hand, been studied in a 20 year old progeny trial in Tiba Prefecture. The average height of the former is about 23 meters, while that of the latter is 8 meters.

Even when we disregard the fact that the concept of heritability is applied to each individual population, and assume that it may be nearly equal in most natural populations of a species, we are still not sure if the heritability

does not change in the course of the ageing or the increase of the height of the trees. Concerning this question, we must also mention that the variation is much larger in the present material than in the previous one (TODA, 1957). In the previous material, the coefficients of variations were 9.3 and 18.3 per cent for tree height and stem girth respectively, while those in the present material are 23.2 and 32.8 per cent respectively. Although variations due to the interaction between rows and columns, which belongs to the macroscopic variation of site condition, may have remained, these figures are much larger than those in the previous material.

The difference may be due to the difference in the genetic nature of the two populations. But it is more likely that the coefficient of variation in a population becomes smaller and smaller as the trees grow, because the population gradually loses its inferior constituents in thinnings. This assumption would not be difficult to examine, because it is sufficient to study the coefficients of variation in various stands of different ages or different average height which are apparently of the same genetic nature. But even if this assumption is true, it is not certain what influences follow in the estimation of heritability.

When the total variance of a population becomes smaller it appears to result in an enlarged estimate of heritability because the denominator in the formula becomes smaller. But the elimination of inferior trees also makes variance due to mother trees smaller and this is the numerator of the formula; thus it is not certain whether the whole function, the estimate of heritability, becomes larger or smaller.

It is not worthwhile discussing this further at present because we have very poor knowledge in this field. So, at present, it is better to accept the two estimates above as being reasonable ones. But, because their accuracy is rather low as the result of the deficiencies in the material, we hope to accumulate as much information as possible to obtain a more reliable estimation.

Summary

The heritability in the narrow sense of tree height and stem girth was estimated in *Cryptomeria*, utilizing a 20 year old progeny trial as the material. The results agreed quite well with the previous estimate made for Scots pine. Comparing them with the corresponding heritability in the broad sense, the authors state that the effect of selection by sexual reproduction must be one half or one third of that of vegetative propagation, and that the importance of heterosis is also confirmed by this study of variation. The changes in variation which accompany the ageing or increase in size of trees are discussed but no conclusion is reached. It is certain that more intensive study and increased information of this field are required.

Zusammenfassung

Titel der Arbeit: *Die Heritabilität von Baumhöhe und Stammumfang bei Cryptomeria nach generativer Reproduktion.*

An einem 20 Jahre alten Nachkommenschaftsversuch von *Cryptomeria japonica* wurde die Heritabilität „im engeren Sinne“ geschätzt. Die erhaltenen Resultate stimmen gut mit einer früher durchgeführten ähnlichen Schätzung bei *Pinus silvestris* überein. Bei einem Vergleich mit der Heritabilität „im weiteren Sinne“ stellt der Autor fest, daß der Selektionserfolg bei generativer Vermehrung nur

etwa $\frac{1}{2}$ bis $\frac{1}{3}$ des bei vegetativer Vermehrung zu erwartenden sein dürfte. Dies ist eine Folge der bedeutenden Heterosis, wie sie in der Variationsuntersuchung nachgewiesen wurde. Weiter werden die Änderungen der Variation mit zunehmendem Alter oder zunehmender Baumgröße diskutiert, aber noch keine Schlußfolgerungen gezogen. Es ist sicher, daß auf diesem Gebiet noch eingehende Untersuchungen und vermehrte Informationen erforderlich sind.

Résumé

Titre de l'article: *L'héritabilité de la hauteur et de la circonférence chez Cryptomeria.*

L'héritabilité au sens strict a été estimée chez la *Cryptomeria*, pour la hauteur et la circonférence, d'après un test de descendance âgé de 20 ans. Les résultats concordent assez bien avec les estimations faites antérieurement pour le Pin sylvestre. En les comparant avec l'héritabilité correspondante, prise au sens large, les auteurs concluent que l'effet de la sélection sur une descendance doit être la

moitié ou le tiers de ce qu'il est sur un clone; d'autre part, l'importance de l'hétérosis est confirmée par cette étude. Les changements dans la variation qui se produisent lorsque l'arbre vieillit et que ses dimensions augmentent sont étudiés, mais aucune conclusion ne peut être donnée. Il est certain qu'une étude plus poussée et des renseignements plus complets sont nécessaires dans ce domaine.

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Grundlagen und Voraussetzungen der autovegetativen Vermehrung

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I. Problemstellung

Die Arbeiten über autovegetative Vermehrung von Waldbäumen haben in den letzten 25 Jahren einen derartigen Umfang angenommen, daß einzelne Autoren listenmäßige Zusammenstellungen angefertigt haben — AVERY und JOHNSON, 1947 (1), VERLEYEN, 1948 (12), LAIBACH und FISCHNICH, 1950 (7), THIMANN und BEHNKE-ROGERS, 1950 (11) und KRÜSSMANN, 1954 (6). Hieraus kann man den Eindruck gewinnen, als hätte die Stecklingsvermehrung bereits den Stand der rezeptmäßigen Anwendung erreicht. Vielfach sind jedoch die Ergebnisse nicht reproduzierbar oder übereinstimmend, wie die Aufstellung von THIMANN-ROGERS bei mehreren Baumarten zeigen. Allein von *Pinus strobus* sind 54 Ergebnisse angeführt, die aber keine klare Gesetzmäßigkeit erkennen lassen. Z. B. bewurzelten sich unbehandelte Kontrollen vom Januar mit 42%, vom Februar mit 4 und 7%, vom März mit 18 und 30% (alle Mutterbäume waren unter 10 Jahre alt!). Die Märzversuche zeigen bei einer Behandlung mit 0,00001% Indolylbuttersäure im dreistündigen Tauchbad 60% Bewurzelung, bei gleicher Konzentration und Tauchzeit mit Naphthyllessigsäure 30%, bei Steigerung der Buttersäurekonzentration auf 0,0002% und einer Tauchzeit von 5 Stunden 70%. Weitere Literaturangaben könnten diese Tatsachen unterstreichen, die allen auf diesem Sektor arbeitenden Forschern aus Erfahrung bekannt sind. Bei den Erörterungen soll nicht unberücksichtigt bleiben, daß Versuche mit biologischen Objekten, insbesondere mit langlebigen Gewächsen, fast immer komplexen Einwirkungen ausgesetzt sind und die Reproduzierbarkeit meist nicht in engen Grenzen angestrebt werden kann. Vielfach liegt aber gerade bei den Arbeiten über autovegetative Vermehrung eine einseitige Betrachtungsweise vor, die die Bedeutung der Wuchsstoffeinwirkung ungebührlich in den Vordergrund schiebt. Der Wuchsstoff ist jedoch nur ein Faktor, der sich wohl-

geordnet in den gesamten Fragenkomplex der Vermehrung einfügen muß. Daher sollen sich die weiteren Ausführungen um die Klärung der Frage bemühen, welche bisher bekannten Faktoren auf die Wurzelbildung einen entscheidenden Einfluß ausüben und welche Steuerungsmöglichkeiten bestehen.

II. Die zu untersuchenden Faktoren

1. Zeitpunkt der Stecklingsentnahme

Bei der Gehölzvermehrung haben sich zwei Schwerpunkte herausgebildet: der Spätwinter und der Hochsommer. Im Spätwinter verwendet man völlig ausgereiftes Holz, das sich eben noch in der Winterruhe befindet, und nützt die rege physiologische Tätigkeit zu Anfang der Vegetationszeit zur Kallus- und Wurzelbildung aus. Im Sommer ist das Gewebe hingegen wesentlich plastischer und bildungsfähiger. Bei Holzpflanzen hängt dieses weitgehend von dem Grad der Verholzung, also der Einlagerung von Lignin und Cellulose in die Zellwände ab. Bei den einzelnen Baumarten stimmt der Verholzungsgrad zeitlich nicht überein, meist sind darüber hinaus innerhalb der Art erhebliche Unterschiede zu erkennen, die neben genotypischer Veranlagung des Einzelbaumes vor allem bei Standorttrassen deutlich ausgeprägt erscheinen.

In der Vermehrungsliteratur wird deshalb der Zeitpunkt des Schneidens und Steckens angegeben. Man wählt hierzu das jeweilige Datum. Dies wäre angängig, wenn die Kalenderbezeichnung in Beziehung zu einer kausalen Größe gesetzt würde. Mit Hilfe mikroskopischer Schnitte und Färbemethoden eine Verbindung von physiologischer Entwicklung zur Datumsangabe zu finden, erwies sich als zu umständlich und fehlerhaft.

Neben der jahreszeitlich bedingten Reife der Triebe wirken noch andere Faktoren auf die Bewurzelungsbereit-