Scientific Reports of the Faculty of Agriculture
Okayama University Vol. 97, 17–24 (2008)

Mathematical Model for the Calculation of Full and Half Sib Covariance in an Artificial Autotetraploid Population Including Aneuploids

Tetsuo Morisawa[a] **and Kenji Kato**
(Course of Applied Plant Science)

For the estimation of genetic variance of an artificial autotetraploid population, a mathematical model of full and half sib covariances between sibs with various chromosome numbers, which were derived from euploid or aneuploid parents, was devised for a case where the inbreeding coefficient of the parents was $F = 0$. The coefficients defined in Kempthorne's model were separated into two parts: (i) A, D, T and Q, and (ii) ϕ and φ. The former four parameters were defined as probabilities of factor combinations, which could be compared between various sibs, for additive, digenic, trigenic, and quadrigenic effects, and were mutually independent. The latter two parameters, which were the numbers of the identical allele and the identical allele pair combinations that two sibs inherited from a parent, were defined as linear functions of the probabilities that two sibs inherited allele or allele pair from a parent, respectively. These probabilities depend on chromosome behavior during meiosis and the chromosome number of the gametes. For the estimation, it was assumed that quadrivalent chromosomes were distributed by 2–2 and 1–3 with probabilities κ and λ ($\kappa + \lambda = 1$), respectively. The distribution of trisomic and pentasomic chromosomes to the poles was assumed to be 1–2 and 2–3. Then, the probabilities were estimated for the simple case where all male and female gametes could equally fertilize irrespective of their chromosome number, provided that tetrasomic chromosomes completely formed a quadrivalent chromosome.

The constitution of variance components were different according to the sib combinations and family. Therefore, for the calculation of the covariance of a family, the covariances between various sibs were averaged by the combination frequency in a family, and for the calculation of the covariance of population, the family's covariances were averaged by the family's frequency in the population.

Key words : artificial autotetraploid, covariance, variance component, euploid, aneuploid

Introduction

Artificial autotetraploid populations in plants generally consist not only of euploids but also of aneuploids, whose percentage ranges from 15% to 60%[3,6,7,14,15,19]. The appearance of aneuploids in such populations is ascribable to the fertilization of aneuploid gametes resulting from an uneven disjunction of multivalent chromosomes in euploid and aneuploid plants. The existence of aneuploids, as well as the double reduction in meiosis, makes the genetic analysis of the quantitative traits very complicated. So far, there have been many reports on the practical and theoretical analysis and on the computer simulation of genetic variances for quantitative traits[1,2,5,10,11,13,14,16,17].

Several methods using covariance between relatives have been reported by Kempthorne[8], Killick[9] and Tan[18]. In these methods, full and half sib families should be analyzed, and thus variance components could be easily calculated based on a suitable experimental design[4]. For populations derived from crosses between pure lines, the methods for the estimations of covariance were presented based on the chromosome segregation model[18] and the chromatid segregation model[9], respectively. Kempthorne[8], based on the chromosome segregation model without interaction between loci, established a general model of covariance between relatives in a random mating population. In these models the covariance can be partitioned into additive and other genetic variance components. However, these reports assumed the ideal population consisted only of euploids, and ignored the frequent occurrence of aneuploids. Since euploids and aneuploids coexist in actual populations, the covari-

Received October 1, 2007
a) *Aki Senior High School*

ance of a family should include the covariances of various combinations of sibs, which should be weighted by the frequency of each combination. Furthermore, the constitution of variance components should be different in various sib combinations in a family, and also different according to families in the population.

In this study, for the calculation of covariances between various sibs, the coefficients defined in Kempthorne's model[8] were separated into two parts: (i) A, D, T and Q, and (ii) ϕ and ψ. The former four parameters were defined as probabilities of factor combinations, which could be compared between various sibs, for additive, digenic, trigenic, and quadrigenic effects and were mutually independent. The latter two parameters, which were the numbers of the identical allele and the identical allele pair combinations that two sibs inherited from a parent, were defined as linear functions of the probabilities (p, q, r, s, u and v) that two sibs inherited allele or allele pair from a parent. These probabilities (p, q, r, s, u and v) depend on the mode of chromosome disjunction in meiosis and the chromosome number of the gametes. The general formula of p, q, r, s, u and v was constructed by using probabilities κ and λ. That quadrivalents were distributed to each pole by 2–2 and 1–3, respectively[6], provided that both male and female gametes could equally fertilize irrespective of their chromosome number and that tetrasomic chromosomes completely formed quadrivalent chromosomes.

The problem that the constitution of variance components should be different according to the sib combination of a family and of the family in the population was solved by averaging the covariances of sibs in the family, and of the family in the population.

Modified Kempthorne Model of Covariances Between Relatives

Let the contribution of each allele at a locus to the genotypic values of autotetraploid sibs y and y' be

$$\begin{aligned} y &= \mu + \alpha_1 + \alpha_2 + \alpha_3 + \alpha_4 + \ldots \\ &\quad + \beta_{12} + \beta_{13} + \beta_{14} + \beta_{23} + \beta_{24} + \beta_{34} + \ldots \\ &\quad + \gamma_{123} + \gamma_{124} + \gamma_{134} + \gamma_{234} + \ldots + \delta_{1234} + \ldots \\ y' &= \mu + \alpha_1' + \alpha_2' + \alpha_3' + \alpha_4' + \ldots \\ &\quad + \beta'_{12} + \beta'_{13'} + \beta'_{14'} + \beta'_{23} + \beta'_{24} + \beta'_{34} + \ldots \\ &\quad + \gamma'_{123} + \gamma'_{124'} + \gamma'_{134} + \gamma'_{234} + \ldots + \delta'_{1234} + \ldots \end{aligned} \quad (1)$$

In this equation, the factor μ is the population mean. α, β, γ, and δ are additive, digenic, trigenic, and quadrigenic effects, which are mutually independent. Their means are equal to 0 and their variances are $V(\alpha)$, $V(\beta)$, $V(\gamma)$ and $V(\delta)$, respectively. The subscript figures indicate the allele concerned. The number of the members of α, β, γ, and δ in the equation depends on the chromosome number. Therefore the coefficients and the constitution of the variance components given in Kempthorne's equation must be changed according to the chromosome number. As the coefficients consist of two parts, they can be separately calculated, considering that the variance components of the covariance of family and population are average components. The equation is changed to the following form:

$$\begin{aligned} \mathrm{Cov}(y,y') = {} & A \cdot (\phi + \phi')\,\sigma_A^2 + D \cdot (\phi\phi' + \psi + \psi')\,\sigma_D^2 \\ & + T \cdot (\phi\psi' + \phi'\psi)\,\sigma_T^2 + Q \cdot (\psi\psi') \cdot \sigma_F^2 \end{aligned} \quad (2)$$

A, D, T, Q: probabilities of factor combinations which can be compared between sibs, for factors α, β, γ, and δ.

ϕ (ϕ'): number of the identical pollen parent (seed parent) allele combinations between two sibs.

ψ (ψ'): number of the identical pollen parent (seed parent) allele pair combinations between two sibs.

σ_A^2, σ_D^2, σ_T^2 and σ_F^2: variance component of additive, digenic, trigenic, and quadrigenic effects. Each variance component should be different according to the type of sib combinations. For the calculation of the covariance of a family, the covariances of various sib combinations must be averaged by the frequency of each combination, since covariances may differ from each other. The covariance of the population can be obtained as the mean of the ovariance of a family, weighted by the frequency of the family in the population. Therefore, the variance components of covariance, σ_A^2, σ_D^2, σ_T^2 and σ_F^2, should be treated as components with an average constitution.

Assumption for Calculation of Covariances

The following four assumptions are made for the calculation of covariances.

1. The segregation is by chromosome rather than by chromatid.
2. The plants are sampled from a random mating equilibrium population with a steady state of eu- and aneruploid frequencies[7,19].
3. There are no interactions between loci.
4. In aneuploids whose chromosome number is less than $4x-1$ and more than $4x+1$, aneuploid chromosomes are non homologous with each other.

The first and third assumptions are also made by Kempthorne (1955)[8].

Result

(I) Calculation of A, D, T and Q

First, the covariance between euploid sibs is calcu-

lated. Since the effect of each factor on the genotype is mutually independent, calculation should be practiced within each factor. For factor α, there can be 16 kinds of allelic combinations between sibs, based on equation (1), and thus the probability of each combination is 1/16. Since comparison between sibs is possible only for four combinations, i.e. α_1 vs. α_1', α_2 vs. α_2', α_3 vs. α_3', α_4 vs. α_4', the probability (A) becomes 1/4 (=4/16). For factors β, γ, and δ, in the same way, the probabilities D, T, and Q become 1/6 (=6/36), 1/4 (=4/16), and 1, respectively. In the combination of 4x−1 vs. 4x, a comparison is possible for only three combinations of additive effects, i.e. α_1 vs. α_1', α_2 vs. α_2', α_3 vs. α_3', respectively. In this combination, for factor α, there can be 12 kinds of allelic combinations between sibs and thus the probability of each combination is 1/12. Therefore the probability (A) becomes 1/4 (=3/12). For factors β, γ, and δ, in the same way, the probabilities D, T, and Q become 1/6 (=3/18), 1/4 (=1/4), and 0 (nothing), respectively. In a similar manner, coefficients A, D, T, and Q between other sibs can be calculated, and the results are summarized in Table 1.

(II) Calculation of ϕ and ψ where the inbreeding coefficient of parent is equal to 0

The autotetraploid plant receives either one, two or three alleles from a pollen parent, and the rest from a seed parent[6]. Considering two sibs in comparison, there can be six types of allelic constitution as shown in Table 2 and Fig. 1.

Calculation of ϕ

ϕ is defined as the number of identical allele combinatons between two sibs. In the case of a parent with four homologues of the critical chromosome (4x), as in the type 1 constitution, both of the sibs inherit two alleles from a pollen parent. Comparison of either of the two alleles between sibs is possible for four allelic combinations, i.e. A_{11} vs. A_{21}, A_{11} vs. A_{22}, A_{12} vs. A_{21}, A_{12} vs. A_{22} in Fig. 1. A_{lm} indicates (l)th (l=1,2) sib and (m) th (m=1,2) pollen parent's allele. The probability that an arbitrary pair of alleles between sibs is identical is 1/4, and the mean number of identical allele combinations becomes 1 (=1/4×4). In the type 2 constitution, comparison is possible for two allelic combinations where two alleles are identical at a probability of 1/4. The mean number of identical allele combinations becomes 1/2 (=1/4×2). In a similar manner, the mean number of identical allele combinations can be calculated for types 3, 4, 5, and 6, being 6/4 (=1/4×6), 3/4 (=1/4×3), 9/4 (=1/4×9), and 1/4 (=1/4×1), respectively. Therefore, ϕ is given in equation (3).

$$\phi_{4x} = p + q/2 + 3r/2 + 3s/4 + 9u/4 + v/4 \qquad (3)$$

where p, q, r, s, u, and v are the probabilities that two

Table 1 Estimates of the coefficients A, D, T, and Q calculated between sibs with different chromosome number

Type of combinations	Parameters			
	A	D	T	Q
4x−1 vs. 4x−1	1/3	1/3	1	0
4x−1 vs. 4x	1/4	1/6	1/4	0
4x−1 vs. 4x+1	1/5	1/10	1/10	0
4x vs. 4x	1/4	1/6	1/4	1
4x vs. 4x+1	1/5	1/10	1/10	1/5
4x+1 vs. 4x+1	1/5	1/10	1/10	1/5

1) A, D, T and Q are probabilities of factor combinations which can be compared between sibs, for factors α, β, γ and δ.

Table 2 Six types of allelic constitution of two autotetraploid sibs

Allelic constitution	No. of alleles received from a parent		Probability[1)]
	sib 1	sib 2	
type 1	2	2	p
2	2	1	q
3	2	3	r
4	3	1	s
5	3	3	u
6	1	1	v

[1)] p + q + r + s + u + v = 1.

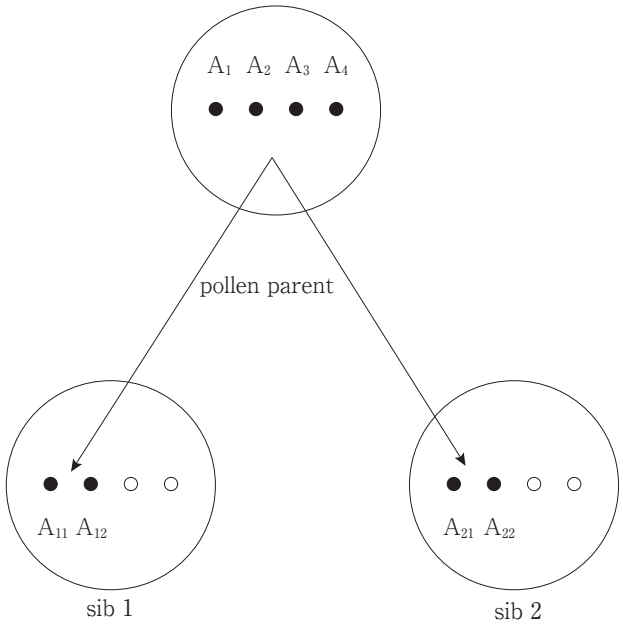

Fig. 1 Type 1 allelic constitution of two autotetraploid sibs in Table 2.
● indicates the pollen's alleles and ○ indicates the seed parent's alleles. A_i (i=1~4) is pollen parent's allele. A_{lm} indicates lth (l=1,2)sib and m th (m=1,2) pollen's allele.

sibs inherit the allele or allele pair from a parent. The subscript of ϕ indicates that a parent has four homologues of the critical chromosome.

In the cases of a parent with three or five homologues of the critical chromosome, the equation for $4x-1$ and $4x+1$ are simply calculated by applying the same method as in equation (3). The equations are:

$$\phi_{4x-1} = 4p/3 + 2q/3 + v/3 \quad (4)$$
$$\phi_{4x+1} = 4p/5 + 6r/5 + 9u/5 \quad (5)$$

As for hypoaneuploids whose chromosome numbers are less than $4x-1$, the deficient chromosomes are non-homologous with each other, and thus they can be considered to have three homologues of the critical chromosome. For this reason, equation (4) is also applicable to most of the hypoaneuploids. In a similar manner, as for hyperaneuploids whose chromosome numbers are more than $4x+1$, equation (5) is also applicable to most of the hyperaneuploids. If the critical genes are not on the aneuploid chromosome, ϕ can be calculated by equation (3).

Calculation of ψ

ψ is defined as the number of identical allele pair combinations between two sibs. However, at least one of the sibs receives only one allele from a parent in types 2, 4, and 6. Therefore, ψ is calculated only for types 1, 3, and 5. In the case of a parent with four homologues of critical chromosome (4x), the probability that two sibs inherit an identical allele pair from a parent is 1/6, since six kinds of allele pair are possible among four parent alleles. There can be 1, 3, and 9 combinations of allele pair, and the mean number of identical allele pair combinations becomes 1/6 ($=1/6\times1$), 1/2 ($=1/6\times3$), and 3/2 ($=1/6\times9$) for types 1, 3, and 5, respectively. Therefore the equation for ψ is:

$$\psi_{4x} = p/6 + r/2 + 3u/2 \quad (6)$$

In the cases of a parent with three or five homologues of critical chromosome, the equations are simply calculated by applying the same method for equation (6). The equations are:

$$\psi_{4x-1} = p/3 \quad (7)$$
$$\psi_{4x+1} = p/10 + 3r/10 + 9u/10 \quad (8)$$

Equation (7) is applicable to hypoaneuploids whose chromosome numbers are less than $4x-1$, by the same reasoning for equation (4). Equation (8) is also applicable to hyperaneuploids whose chromosome numbers are more than $4x+1$, by the same reasoning for equation (5).

(III) Calculation of the probability of allelic constitution of two sibs

For quadrivalent chromosomes, disjunction to the poles can be 2–2 and 1–3 at anaphase I, with the probabilities of κ and λ ($\kappa+\lambda=1$), respectively. Distribution of trisomic and pentasomic chromosomes is assumed as 1–2 and 2–3, respectively, with the probabilities equal to 1[6].

The probability of an allelic constitution of two sibs can be calculated by assuming that the fertilizing ability of the gametes is not affected by their chromosome number and that tetrasomic chromosomes completely form quadrivalent chromosomes. When parents and offspring are all euploid, there are 6 kinds of allelic constitutions between two 4x sibs, as shown in Table 2 and Fig. 1. As for type (1), the probability that both sibs inherit two alleles from a pollen parent is $p=\kappa \times \kappa = \kappa^2$, since a gamete with two critical chromosomes is produced at a probability of κ. The number of alleles inherited from a seed parent is automatically settled by those from a pollen parent. For example, in type (1), the number of alleles is two for both sibs, therefore the probability is $p_{\text{seed parent}} = p_{\text{pollen parent}}$. The probability can be similarly calculated for other types of allelic constitution. Each probability is shown in Table 3-(4).

On the other hand, in cases where the critical chromosome is involved in aneuploidy, these probabilities must be calculated by taking the frequency of different chromosome disjunction types into consideration. As an example, 4x offsprings derived from a cross between $4x-1$ parents were examined. The disjunction of trisomic chromosome is 1–2 as mentioned above, and thus there are no individuals which inherit three homologues from either parent. Therefore the probability that two sibs inherit two homologues from a pollen parent and a seed parent is $p_{\text{pollen parent}}=1$, $p_{\text{seed parent}}=p_{\text{pollen parent}}$, respectively, as shown in Table 3-(4).

Considering the plants whose chromosome number ranges from $4x-1$ to $4x+1$, there can be six combinations of chromosome numbers among the offspring derived from nine cross combinations. The probabilities were calculated for these sibs in a similar manner and the results are summarized in Table 3. In cases where the fertilization ability of the gametes is affected by their chromosome number, the probability of these allelic constitutions must be corrected by their ability. The probabilities calculated for $4x+1$ (or $4x-1$) sibs are also applicable to $4x\pm k$ ($k=2,3...$) sibs, since the additional (or deficient) chromosomes are non homologous with each other.

(IV) Examples

In the first case, full and half sib covariances between

4x sibs derived from 4x × 4x cross are calculated,by assuming that only 2x pollen and ovule contribute to the fertilization. The allelic constitution of two sibs is considered as type 1 (Table 2). Therefore, probabilities are p = 1 in both parents ($\kappa = 1$ in Table 3-(4)). The values of ϕ, ψ, ϕ', and ψ' are 1, 1/6, 1, and 1/6, respectively. Thus full and half sib covariances can be calculated by equation (2), using parameters for 4x vs. 4x given in Table 1 and these values. The results are:

$$\mathrm{Cov}\ (\mathrm{FS}) = \sigma_A^2/2 + 2\sigma_D^2/9 + \sigma_T^2/12 + \sigma_F^2/36 \quad (9)$$

$$\mathrm{Cov}\ (\mathrm{HS}) = \sigma_A^2/4 + \sigma_D^2/36 \quad (10)$$

Table 3 The estimates of the probabilities (p, q, r, s, u, and v) of allelic constitution of two sibs whose chromosome number ranged from 4x − 1 to 4x + 1

Chromosome number of polle parent	Chromosome number of seed parent																	
	4x−1						4x						4x+1					
	p	q	r	s	u	v	p	q	r	s	u	v	p	q	r	s	u	v
(1) offspring 4x − 1 vs. 4x − 1																		
4x − 1 p. p.	1/4	1/2	—	—	—	1/4	1/4	1/2	—	—	—	1/4	—	—	—	—	—	1
s. p.	1/4	1/2	—	—	—	1/4	1/4	1/2	—	—	—	1/4	1	—	—	—	—	—
4x p. p.	κ^2	$\kappa\lambda$	—	—	—	$\lambda^2/4$	κ^2	$\kappa\lambda$	—	—	—	$\lambda^2/4$	—	—	—	—	—	1
s. p.	$\lambda^2/4$	$\kappa\lambda$	—	—	—	κ^2	$\lambda^2/4$	$\kappa\lambda$	—	—	—	κ^2	1	—	—	—	—	—
4x+1 p. p.	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
s. p.	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—
(2) offspring 4x−1 vs. 4x																		
4x − 1 p. p.	1/2	1/2	—	—	—	—	1/4	1/2	—	—	—	1/4	—	1/2	—	—	—	1/2
s. p.	1/2	1/2	—	—	—	—	1/4	1/4	1/4	1/4	—	—	1/2	—	1/2	—	—	—
4x p. p.	κ^2	$\kappa\lambda/2$	$\kappa\lambda/2$	$\lambda^2/4$	—	—	κ^2	$\kappa\lambda$	$\kappa\lambda/2$	$\lambda^2/4$	—	$\lambda^2/4$	—	$\kappa\lambda/2$	—	—	—	$\lambda^2/4$
s. p.	$\kappa\lambda/2$	$\kappa^2+\lambda^2/4$	—	—	—	$\kappa\lambda/2$	$\kappa\lambda/2$	$\kappa^2+\lambda^2/4$	$\lambda^2/4$	$\kappa\lambda/2$	—	$\kappa\lambda/2$	$\kappa\lambda/2$	—	$\lambda^2/4$	—	—	—
4x + 1 p. p.	1/2	—	1/2	—	—	—	1/2	—	1/2	—	—	—	—	—	—	—	—	—
s. p.	—	1/2	—	—	—	1/2	—	1/2	—	—	—	1/2	—	—	—	—	—	—
(3) offspring 4x − 1 vs. 4x + 1																		
4x − 1 p. p.	—	—	—	—	—	—	1/2	1/2	—	—	—	—	—	1	—	—	—	—
s. p.	—	—	—	—	—	—	—	—	1/2	1/2	—	—	—	—	1	—	—	—
4x p. p.	—	—	$\kappa\lambda/2$	$\lambda^2/4$	—	—	κ^2	$\kappa\lambda/2$	$\kappa\lambda/2$	$\lambda^2/4$	—	—	—	$\kappa\lambda/2$	—	$\lambda^2/4$	—	—
s. p.	$\lambda^2/4$	$\kappa\lambda/2$	—	—	—	—	$\lambda^2/4$	$\kappa\lambda/2$	$\kappa\lambda/2$	κ^2	—	—	$\lambda^2/4$	—	$\kappa\lambda/2$	—	—	—
4x+1 p. p.	—	—	1	—	—	—	1/2	—	1/2	—	—	—	—	—	—	—	—	—
s. p.	—	1	—	—	—	—	—	1/2	—	1/2	—	—	—	—	—	—	—	—
(4) offspring 4x vs. 4x																		
4x − 1 p. p.	1	—	—	—	—	—	1/4	1/2	—	—	—	1/4	1/4	1/2	—	—	—	1/4
s.p.	1	—	—	—	—	—	1/4	—	1/2	—	1/4	—	1/4	—	1/2	—	1/4	—
4x p. p.	κ^2	—	$\kappa\lambda$	—	$\lambda^2/4$	—	κ^2	$\kappa\lambda$	$\kappa\lambda$	$\lambda^2/2$	$\lambda^2/4$	$\lambda^2/4$	κ^2	$\kappa\lambda$	—	—	—	$\lambda^2/4$
s.p.	κ^2	$\kappa\lambda$	—	—	—	$\lambda^2/4$	κ^2	$\kappa\lambda$	$\kappa\lambda$	$\lambda^2/2$	$\lambda^2/4$	$\lambda^2/4$	κ^2	—	$\kappa\lambda$	—	$\lambda^2/4$	—
4x + 1 p. p.	1/4	—	1/2	—	1/4	—	1/4	—	1/2	—	1/4	—	1	—	—	—	—	—
s. p.	1/4	1/2	—	—	—	1/4	1/4	1/2	—	—	—	1/4	1	—	—	—	—	—
(5) offspring 4x vs. 4x + 1																		
4x − 1 p. p.	—	—	—	—	—	—	1/2	1/2	—	—	—	—	1/2	1/2	—	—	—	—
s. p.	—	—	—	—	—	—	—	—	1/2	—	1/2	—	—	—	1/2	—	1/2	—
4x p. p.	—	—	$\kappa\lambda/2$	—	$\lambda^2/4$	—	κ^2	$\kappa\lambda/2$	$\kappa\lambda$	$\lambda^2/4$	$\lambda^2/4$	—	κ^2	$\kappa\lambda/2$	$\kappa\lambda/2$	$\lambda^2/4$	—	—
s. p.	$\kappa\lambda/2$	$\lambda^2/4$	—	—	—	—	$\kappa\lambda/2$	$\lambda^2/4$	$\kappa^2+\lambda^2/4$	$\kappa\lambda/2$	$\kappa\lambda/2$	—	$\kappa\lambda/2$	—	$\kappa^2+\lambda^2/4$	—	$\kappa\lambda/2$	—
4x + 1 p. p.	—	—	1/2	—	1/2	—	1/4	—	1/2	—	1/4	—	1/2	—	1/2	—	—	—
s.p.	1/2	1/2	—	—	—	—	1/4	1/4	1/4	1/4	—	—	1/2	—	1/2	—	—	—
(6) offspring 4x+1 vs. 4x+1																		
4x − 1 p. p.	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—
s. p.	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—
4x p.p.	—	—	—	—	1	—	κ^2	—	$\kappa\lambda$	—	$\lambda^2/4$	—	κ^2	—	$\kappa\lambda$	—	$\lambda^2/4$	—
s. p.	1	—	—	—	—	—	$\lambda^2/4$	—	$\kappa\lambda$	—	κ^2	—	$\lambda^2/4$	—	$\kappa\lambda$	—	κ^2	—
4x + 1 p. p.	—	—	—	—	1	—	1/4	—	1/2	—	1/4	—	1/4	—	1/2	—	1/4	—
s. p.	1	—	—	—	—	—	1/4	—	1/2	—	1/4	—	1/4	—	1/2	—	1/4	—

1) The probabilities should be divided by row totals of each family except right upside and left downside marginal blocks, where pollen parent is 4x.
2) The "p. p." and "s. p." indicate the pollen parent's and seed parent's alleles.

In the second case, full and half sib covariances between 4x sibs derived from the crosses $4x \times 4x$, $4x-1 \times 4x$, and $4x+1 \times 4x$ are calculated, by assuming that $\kappa = 0.8$ and $\lambda = 0.2$[6,19]. The allelic constitutions of sibs are from type 1 to type 6 in Table 2. The probabilities (p, q, r, s, u, and v) can be calculated by using $\kappa = 0.8$ and $\lambda = 0.2$ in Table 3–(4). The values of ϕ, ψ, ϕ', and ψ' calculated by equations (3)～(8) are summarized in Table 4.

Full sib covariance can be calculated by equation (2), using parameters for 4x vs. 4x given in Table 1 and those in Table 4. The results are:

$$4x \times 4x \quad : \mathrm{Cov}(FS) = 0.500\sigma_A^2 + 0.233\sigma_D + 0.100\sigma_T^2 + 0.040\sigma_F^2 \quad (11)$$

$$4x-1 \times 4x : \mathrm{Cov}(FS) = 0.575\sigma_A^2 + 0.468\sigma_D^2 + 0.147\sigma_T^2 + 0.065\sigma_F^2 \quad (12)$$

$$4x+1 \times 4x : \mathrm{Cov}(FS) = 0.445\sigma_A^2 + 0.179\sigma_D^2 + 0.062\sigma_T^2 + 0.020\sigma_F^2 \quad (13)$$

Half sib covariance between sibs with a common pollen parent can be calculated in a similar manner. In this case ϕ' and ψ' have to be 0. The results are:

$$4x \times 4x \quad : \mathrm{Cov}(HS) = 0.250\sigma_A^2 + 0.033\sigma_D^2 \quad (14)$$

$$4x-1 \times 4x : \mathrm{Cov}(HS) = 0.278\sigma_A^2 + 0.042\sigma_D^2 \quad (15)$$

$$4x+1 \times 4x : \mathrm{Cov}(HS) = 0.223\sigma_A^2 + 0.022\sigma_D^2 \quad (16)$$

Discussion

Variance components of covariance between 4x sibs are $\sigma_A^2 = 4V(\alpha)$, $\sigma_D^2 = 6V(\beta)$, $\sigma_T^2 = 4V(\gamma)$, and $\sigma_F^2 = V(\delta)$. On the other hand, those between $4x-1$ and 4x sibs are $\sigma_A^2 = 3V(\alpha)$, $\sigma_D^2 = 3V(\beta)$, $\sigma_T^2 = V(\gamma)$, and $\sigma_F^2 = 0$, and those between $4x+1$ and 4x sibs are $\sigma_A^2 = 4V(\alpha)$, $\sigma_D^2 = 6V(\beta)$, $\sigma_T^2 = 4V(\gamma)$, and $\sigma_F^2 = V(\delta)$, since the constitution of variance components is determined by the smaller number of the members of α, β, γ, and δ in the equation (1). In a similar manner, variance components of any combinations are equal to the variance components of the sib with a smaller chromosome number. Therefore, for the calculation of the covariance of a family, these covariances must be averaged by their combination frequency in a family. The covariance of a population can be obtained as the mean of the covariance of a family, weighted by the frequency of the family in the population. The constituion of the variance component, therefore, must be considered as the average constitution.

Table 4 The estimates of ϕ, ψ, ϕ', and ψ' calculated for 4x sibs, in case of $\kappa = 0.8$ ($\lambda = 0.2$)

Parameters	Cross combination		
	$4x \times 4x$	$4x-1 \times 4x$	$4x+1 \times 4x$
ϕ	1.00	1.11	0.89
ψ	0.20	0.25	0.13
ϕ'	1.00	1.19	0.89
ψ'	0.20	0.26	0.15

1) ϕ (ϕ') is number of the identical pollen parent (seed parent) allele combinations between two sibs.
2) ψ (ψ) is number of the identical pollen parent (seed parent) allele pair combinations between two

For example, the equations (9) and (10) are also covariances, in a case where only euploid chromosomes contribute to the trait, and coincide with Kempthorne's results defined for euploid sibs ($\sigma_A^2 = 4V(\alpha)$, $\sigma_D^2 = 6V(\beta)$, $\sigma_T^2 = 4V(\gamma)$, and $\sigma_F^2 = V(\delta)$)[8]. Covariances from (11) to (16) are calculated, in cases where all kinds of gametes produced by parents contribute to the fertilization, and where only aneuploid chromosome contributes to the trait. In these cases, the coefficients of each variance component of the covariance proved to be different between families. This is the reason why ϕ and ψ are different among both parents. Therefore, to obtain the 4x full sib covariance in a $4x \times 4x$ family, the covariances calculated by equations (9) and (11) have to be averaged by the probabilities that a set of homologous chromosomes is or is not involved in aneuploidy, respectively. As to $4x-1 \times 4x$ family, those calculated by equations (9) and (12) must be averaged by the same way. In a similar manner, covariances of various sib combinations in a family can be calculated.

The covariance of a family can be calculated as the mean of the covariances of various combinations of sibs which should be weighted by their combination frequency. The actual frequency of euploids and various types of aneuploids are different among the crops, i.e. Lettuce[3], Artemicia[15], Japanese radish[19], Renge[6,7], and Rye grass[14]. The frequency of each combination can be estimated by the distribution of chromosome number in a family, as indicated by many reports[3,6,7,14,15,19]. The covariance of the population can be obtained as the mean of the covariance of a family. Therefore, the variance components of the covariance of a population must be treated as components with an average constitution.

Covariance in practical populations may include the variance due to the effects of genotype and the chromosome number itself. Therefore the experimental design should be established to divide the covariance into variance components ascribable to genotype and chromosome number. Factorial design to use a mating system, where only 2x pollen fertilize with $2x \pm k$ ($k = 0, 1, \ldots$) female gametes, is suitable as an experimental design. In this design, the families derived from this mating system must be arranged in two ways: seed parent and off-

spring chromosome numbers. Therefore the effects of genotype and of chromosome numbers can be calculated by analysis of variance. The details will be given elsewhere.

In the case where the segregation is by chromatid rather than chromosome, the genotypic frequency of gametes will be influenced by double reduction in euploid and complicated segregation in aneuploid[12]. Therefore the equations of ϕ and ψ may be different from those in the case of chromosome segregation. Construction of ϕ and ψ, including these factors, is under investigation.

Acknowledgements

This study was originally planned as a collaborative work with the late Dr. K. Hayashi, former Professor of Kochi University, to whom the author expresses his appreciation.

References

1) Dessureaux, L. : Introduction to the autotetraploid diallel. Can. J. Genet. Cytol., **1**, 94–101 (1959)
2) Doyle, G. G. : Autotetraploid gene segregation. Theor. Appl. Genet., **43**, 139–146 (1973)
3) Eineet, J. : Aneuploidy in relation to partial sterility in autotetraploid lettuce. Amer. J. Bot., **34**, 99–105(1947)
4) Gallais, A. : Analysis of variance components of testcross progenies in an autotetraploid species and consequences for recurrent selection with a tester. Theor. Appl. Genet., **83**, 353–359 (1992)
5) Hague, L. M. and R. N. Jones : Cytogenetics of *Lolium perene*. 4. Colchicine induced variation in diploid. Theor. Appl. Genet., **74**, 233–241 (1987)
6) Hayashi, K. : Studies on the mechanism of partial sterility in induced autotetraploid of renge (*Astragalus sinicus* L.). Mem. Fac. Agr. Kochi Univ., **28**, 1–68 (1974)
7) Hayashi, K. and T. Morisawa : The estimation of aneuploid frequencies in the progenies of induced autotetraploid Renge (*Astragalus sinicus* L.). Res. Rep. Kochi Univ., Agr. Sci., **12**, 125–133 (1977)
8) Kempthorne, O. : The correlation between relatives in simple autotetraploid population. Genetics, **40**, 168–174 (1955)
9) Killick, R. J. : The biometrical genetics of autotetraploids. I. Generations derived from a cross between two pure lines. Heredity, **27**, 331–346 (1971)
10) Klinga, K. : Aneuploidy induced autotetraploid population of *Festuca pratensis*, *Lolium multiflorum* and *Lolium perene*. I. The frequency of aneuploids and performance of spaced plants in two autotetraploid populations of *Festuca pratensis*. Hereditas, **104**, 75–83 (1986)
11) Klinga, K. : Aneuploidy induced autotetraploid population of *Festuca pratensis*, *Lolium multiflorum* and *Lolium perene*. III. Performance of plant at different sowing densities in a perennial sward of tetraploid *Festuca pratensis*. Hereditas, **106**, 277–287 (1987)
12) Mather, K. : Segregation and linkage in autotetraploids. J. Genet., **32**, 287–314 (1936)
13) Simonsen, ϕ. : Genetic variation in diploid and autotetraploid population of *Lolium perene* L. Hereditas, **84**, 133–156 (1976)
14) Simonsen, ϕ. : Genetic variation in diploid and autotetraploid population of *Festuca pratensis*. Hereditas, **85**, 1–24 (1977)
15) Suzuka, O., S. Koriba and S. Mitsuoka : Studies on tetrapliod *Arutemicia Kurranenensis Quazalibash* induced by colchicine treatment. Seiken Ziho, **7**, 63–67 (1955)
16) Swanson, J., W. Dudley and S. G. Cramer : Simulated selection in autotetraploid population. I. Computer methods and effect of linkage. Crop. Sci., **14**, 625–630 (1974a)
17) Swanson, J., W. Dudley and S. G. Cramer : Simulated selection in autotetraploid population. II. Effect of double reduction, population size, and selection intensity. Crop. Sci., **14**, 630–636 (1974b)
18) Tan, W. Y. : On the biometrical genetics of autotetraploids from a cross between two pure lines. Bot. Bull. Academia Sinica, **17**, 1–17 (1976)
19) Tokumasu, S. : The maintenance and collapse of polyploidy in the progenies of autotetraploid Japanese radishes, with reference to the occurrence of aneuploid plants. Mem. Ehime Univ. Sect., VI **7**, 177–349 (1961)

人為同質４倍体集団における全兄弟及び半兄弟共分散の数学モデル

森 澤 徹 男[a)]・加 藤 鎌 司
（応用植物科学コース）

人為同質４倍体集団の遺伝分散を求めるため，両親が近交系数Ｆ＝０の同質４倍体家族の全兄弟と半兄弟の共分散を検討した．Kempthorne のモデルにおいて定義された分散の係数を①Ａ，Ｄ，Ｔ，Ｑと②ϕ，ψの２つに分割した．①は互いに独立な相加，２遺伝子，３遺伝子，４遺伝子効果の組み合わせの確率である．②は兄弟が片親から受け取る同一対立遺伝子の数と対立遺伝子ペアの数である．これは兄弟が片親から対立遺伝子と対立遺伝子の組を受け取る確率の関数であり，この確率は減数分裂での染色体行動と配偶子の染色体数によって決まる．

この確率を推定するため，Ⅳ価染色体は確率κ，λ（$\kappa+\lambda=1$）で２－２と１－３で分配され，Ⅲ価染色体とⅤ価染色体は１－２と２－３に分配されると仮定した．本報告では，四染色体が完全にⅣ価染色体を形成するとして，全ての雌雄の配偶子がその染色体数に関係なく受精できる単純な場合について検討した．

共分散の分散成分の構造は兄弟の組み合わせと家族によって異なる．したがって，家族の共分散は各兄弟の共分散とその組み合わせ頻度を用い平均すれば求めることができ，集団の平均の共分散は家族の共分散と集団での家族の頻度を用い平均すれば求めることができる．

a）高知県立安芸高等学校