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Calculation of Full and Half Sib Covariances in an Artificial Autotetraploid Population Including Aneuploids, in *Astragalus Sinica* L.

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Full and half sib covariances were investigated in an artificial autotetraploid population with random mating in *Astragalus sinicus* L.. Since a set of homologous chromosomes is not necessarily involved in aneuploidy, the covariances must be averaged for two cases, that is, with and without involvement. To average the covariances, the probability that a set of homologous chromosomes was involved in aneuploidy was assumed as 3/8, where "8" and "3" represent the chromosome number of a genome and the mean number of quadrivalent chromosomes formed in a euploid, respectively. The covariances were calculated under the assumption that quadrivalent chromosomes were distributed to the poles by 2-2 and 1-3 with probabilities $\kappa = 0.8$ and $\lambda = 0.2$ ($\kappa + \lambda = 1$) respectively, and that trisomic and pentasomic chromosomes were distributed by 1-2 and 2-3 both with a probability of 1. It was also assumed that the inbreeding coefficient of the parents was $F = 0$, and that 2x and 2x + 1 pollens and all female gametes could fertilize equally. The covariance of a family was taken as an average of the covariance of each sib combination in a family. As a result, the covariance of a population could be obtained as an average of the covariance of each family in a population. The coefficients of variance components calculated under these assumptions were different from those calculated under the same condition except that 2x + 1 pollen could not fertilize. Differences in the coefficient of additive genetic variance components were about 3.3% and 7.2% for full and half sib covariances, respectively. Coefficients of the other variance components were also different between the two cases. However, 2x + 1 pollen could rarely fertilize, since their ability to fertilize in a practical population were lower than 2x pollen. Therefore, it would be valid to calculate full and half sib covariances in an artificial autotetraploid population of *Astragalus sinicus* L. under the condition thatonly 2x pollen could fertilize.

Key words : full and half sib covariances, quadrivalent chromosomes, additive genetic variance, covariance of a family, covariance of a population

Introduction

Genetic variance in an autotetraploid population can be estimated by using covariances between relatives. In a previous paper[21)], the mathematical model of covariance between sibs including aneuploids was reported, and several parameters necessary for the calculation of covariances between sibs were estimated for each combination of sibs with various chromosome numbers, considering euploids and aneuploids in the population. However, for the practical calculation of covariances of an artificial autotetraploid population in *Astragalus sinicus* L, it is further necessary to introduce four factors, namely the probability of quadrivalent chromosome formation in MI, the fertilization ability of gametes, and distribution of eu- and aneuploids in a family, and of the family in an equilibrium population.

Chromosome behavior during the meiosis of tetraploids was reported by Tokumasu[27)], Hayashi[12)], Giraldez and Santos[10)], Benavente and Orellana[1)], Chatterjee and Jenkins[4)], and Khazanehdari et al.[16)]. According to these reports, many bivalent and a few quadrivalent chromosomes are formed, while pentavalent, trivalent, and univalent chromosomes are rarely formed in MI. Based on the observation of euploids in artificial autotetraploid population of *Astragalus sinicus* L. ($n = 8$), Hayashi[12)] reported that about three quadrivalent chromosomes were formed and distributed to the poles by 2-2 and 1-3 with probabilities $\kappa = 0.825$ and $\lambda = 0.175$ ($\kappa + \lambda = 1$), respectively. It was therefore indicated that only a few quadrivalent chromosomes caused aneuploidy, and that

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aneuploid chromosomes were not necessarily responsible for the trait in concern. Thus covariance between sibs must be taken as an average of the covariances calculated for each case. The probability to average the covariance is equal to the frequency of quadrivalent chromosome in MI.

Hayashi and Kiwata[14] reported that 2x and 2x + 1 pollens could fertilize, based on the observation of artificial autotetraploid in *Astragalus sinicus* L.. On the other hand, Kihara et al.[17], Hayashi and Kiwata[14], and Zhang et al.[29] reported that ovules including euploid and aneuploid chromosome numbers have an almost equal fertilization ability. Therefore, the contribution of aneuploid pollens to covariances must be evaluated by comparing the effect of these pollens.

Full and half sib covariances of a family are influenced by the frequency of eu- and aneuploids, since the chromosome distribution of offspring depend on the combination of parents[12,13,14]. Therefore the covariance of a family must be taken as an average of the covariance of each sib combination in a family. As a result, the covariance of a population can be obtained as an average of the covariance of each family in a population.

In this report, the covariance of an artificial autoteraploid population of *Astragalus cinicus* L. was established under the condition that the inbreeding coefficient of the parents was equal to 0, and each chromosome was involved in aneuploidy at a probability of 3/8, where "8" and "3" represent the chromosome number of a genome and the mean number of quadrivalent chromosomes in MI of euploid. Furthermore to evaluate the effect of aneuploid pollens, the covariances were compared for two cases where 2x and 2x + 1 pollens[14] and only 2x pollen could fertilize.

Covariance Between Sibs

In the present study, $\mathrm{Cov\ (FS)_s}$, $\mathrm{Cov\ (HS)_s}$, $\mathrm{Cov\ (FS)_d}$, and $\mathrm{Cov\ (HS)_d}$ indicate the covariances between full and half sibs, respectively, and the subscript "s" and "d" indicate same and different numbers of chromosomes, respectively. $\mathrm{Cov\ (FS)_{aneu}}$, $\mathrm{Cov\ (HS)_{aneu}}$, $\mathrm{Cov\ (FS)_{eu}}$, and $\mathrm{Cov\ (HS)_{eu}}$ are the covariances between sibs with aneuploid and euploid numbers of the critical chromosome, respectively.

The covariances between sibs of an artificial autotetraploid population of *Astragalus sinicus* L. can be calculated by using ν and ξ $(\nu + \xi = 1)$ which are the probabilities of aneuploid (ν) and euploid (ξ) for the critical chromosome in parents. Therefore, the covariances of population, $\mathrm{Cov\ (FS)_p}$ and $\mathrm{Cov\ (HS)_p}$, must be weighted by these probabilities, as follows;

$$\mathrm{Cov\ (FS)_p} = \nu \mathrm{Cov\ (FS)_{aneu}} + \xi \mathrm{Cov\ (FS)_{eu}} \qquad (1)$$

$$\mathrm{Cov\ (HS)_p} = \nu \mathrm{Cov\ (HS)_{aneu}} + \xi \mathrm{Cov\ (HS)_{eu}} \qquad (2)$$

The actual value of ν should be equal to 3/8 in artificial autotetraploid of *Astragalus sinicus* L., if all chromosomes are randomly involved in aneuploidy[12]. In plant species whose chromosomenumber of the genome ranges from 7 to 12, ν is nearly equal to "3/n", where "n" is the chromosome number of a genome[12,19,22,26,28].

In this investigation, $\mathrm{Cov\ (FS)_s}$, $\mathrm{Cov\ (FS)_d}$, $\mathrm{Cov\ (HS)_s}$, and $\mathrm{Cov(HS)_d}$ were calculated under the assumption that quadrivalent chromosomes were distributed to the poles by 2–2 and 1–3 with probabilities $\kappa = 0.8$ and $\lambda = 0.2$ $(\kappa + \lambda = 1)$ respectively, and that trisomic and pentasomic chromosomes were distributed by 1–2 and 2–3 both with a probability of 1. It was also assumed that the inbreeding coefficient of the parents was $F = 0$. Furthermore to evaluate the effect of aneuploid pollens, the covariances were calculated for two cases where only 2x pollen and both 2x and 2x + 1 pollens could fertilize with x～3x ovules[5,6,14,17,18,20,23,25,29]. The covariances of a population were calculated by considering 4x and 4x ± 1 individuals in a population, since the frequencies of 4x ± 2 individuals were very low in an equilibrium population of *Astragalus sinicuas* L.[13].

In the first place, the covariance of each family was calculated as an average of covariance of each sib combination in a family, since chromosome distribution of offspring depends on the combination of parents[12,13,14]. Secondly, the covariance of a population was calculated as an average of covariance of each family in a population. Variance between families includes the covariances between sibs, as indicated by the analysis of variance[7,8]. Therefore variance components of the covariances can be calculated, if the estimated covariances of the population averaged for all families are equivalent to the actual covariances calculated by the analysis of variance.

Results

In the case where aneuploid chromosome does not concern the trait, the covariances are equivalent to those between 4x sibs derived from a 4x × 4x cross, since 4x sibs usually have four homologues of each chromosome[15,21]. Therefore the covariances between sibs are:

$$\mathrm{Cov\ (FS)_{eu}} = 0.500 s_A^2 + 0.222 s_D^2 + 0.083 s_T^2 + 0.028 s_F^2 \qquad (3)$$

$$\mathrm{Cov\ (HS)_{eu}} = 0.250 s_A^2 + 0.028 s_D^2 \qquad (4)$$

These equations hold in all combinations of parents and offspring.

As a simple case, the covariances were calculated under the conditions that only 2x pollen could fertilize and that all ovules could equally fertilize irrespective of their chromosome number. Let only an aneuploid chromosome contribute to the trait. The number of the critical chromosome depends on cross combinations, i.e. from 3 to 5 in 4x seed parent families, from 3 to 4 in 4x − 1 seed parent families, and from 4 to 5 in 4x + 1 seed parent families.

The covariances between sibs, with the same or different chromosome number, can be calculated by using four parameters A, D, T, and Q, and two parameters ϕ and ψ. The former four parameters are the probabilities of genetic factor combinations that can be compared between sibs. The latter two parameters are the number of the identical allele and the identical allele pair combinations between sibs, and can be calculated by using the probabilities p, q, r, s, u, and v that two sibs inherit the allele or allele pair from a parent[21]. Coefficients of variance components of full sib covariances with the same chromosome numbers in 4x × 4x family is given in the following manner. Since two alleles are inherited from 4x pollen parent, the probability is 1 $(p = 1)$ for the pollen alleles. The number of alleles inherited from the seed parent are automatically settled, depending on the chromosome number of the sib, and thus the probability should be either p, q, r, s, u or v, and equal to 1. The combinations of the sib's critical chromosome numbers are 5 vs. 5, 4 vs. 4, and 3 vs. 3 in this family. As for the combination of 5 vs. 5, the probabilities should be $p_{\text{pollen parent}} = 1.000$ and $u_{\text{seed parent}} = 1.000$ respectively, as shown in Table 3-(6)[21]. The probabilities should be calculated for 4 vs. 4 and 3 vs. 3 in a similar manner. Based on these probabilities, ϕ, ψ, ϕ', and ψ' can be calculated by using equations (3) and (6) in Morisawa and Kato[21], and the results are given in Table 1. The coefficients of the variance components for each combination can be obtained by equation (2), using the A, D, T, and Q in Table 1 in Morisawa and Kato[21]. The results are given in Table 2. The coefficients of the variance components of this family can be calculated as an average of these values weighted by the combination frequencies of individuals in a family, i.e. the combination frequency is $\lambda^2/4$ $(= 0.01)$ for 5 vs. 5, since the frequency of individuals with 5 critical chromosomes is $\lambda/2$ $(= 0.1)$. The coefficients of variance components of other families can be obtained in a similar manner. The results for each family are given in Table 3. Therefore, covariance between sibs with the same chromosome number in a population is obtained as an average of these covariances, weighted by the frequency of each family in a population. The frequencies of 4x − 1, 4x, and 4x + 1 are 0.094, 0.712, and 0.194 in an equilibrium population of *Astragalus sinicus* L.[13]. The result is given

Table 3 **Coefficients of variance components of full sib covariances with same chromosome numbers in 4x ± a × 4x ± a families in case of fertilization by only 2x pollen (a = 0, 1)**

Pollen parent	Seed parent			
	4x − 1 (0.094)*	4x (0.712)	4x + 1 (0.194)	mean
additive				
4x − 1 (0.094)*	0.306	0.386	0.290	0.360
4x (0.712)	0.257	0.331	0.223	0.303
4x + 1 (0.194)	0.228	0.203	0.255	0.215
mean	0.256	0.311	0.236	0.291
digenic				
4x − 1 (0.094)	0.167	0.203	0.153	0.190
4x (0.712)	0.118	0.147	0.116	0.138
4x + 1 (0.194)	0.093	0.118	0.096	0.111
mean	0.118	0.147	0.116	0.138
trigenic				
4x − 1 (0.094)	0.083	0.112	0.057	0.099
4x (0.712)	0.049	0.055	0.045	0.052
4x + 1 (0.194)	0.019	0.039	0.033	0.036
mean	0.046	0.057	0.044	0.053
quadrigenic				
4x− 1 (0.094)	0.028	0.037	0.018	0.032
4x (0.712)	0.014	0.018	0.012	0.016
4x + 1 (0.194)	0.020	0.037	0.007	0.030
mean	0.016	0.023	0.012	0.020

* : Frequency of individual in an equilibrium population

in equation (5) and in Table 3. Equations (6), (7), and (8) can be calculated similarly.

$$\mathrm{Cov}\ (\mathrm{FS})_{\mathrm{s}} = 0.291\sigma_{\mathrm{A}}{}^{2} + 0.138\sigma_{\mathrm{D}}{}^{2} + 0.053\sigma_{\mathrm{T}}{}^{2} + 0.020\sigma_{\mathrm{F}}{}^{2} \quad (5)$$

$$\mathrm{Cov}\ (\mathrm{FS})_{\mathrm{d}} = 0.168\sigma_{\mathrm{A}}{}^{2} + 0.061\sigma_{\mathrm{D}}{}^{2} + 0.019\sigma_{\mathrm{T}}{}^{2} + 0.004\sigma_{\mathrm{F}}{}^{2} \quad (6)$$

$$\mathrm{Cov}\ (\mathrm{HS})_{\mathrm{s}} = 0.152\sigma_{\mathrm{A}}{}^{2} + 0.021\sigma_{\mathrm{D}}{}^{2} \quad (7)$$

$$\mathrm{Cov}\ (\mathrm{HS})_{\mathrm{d}} = 0.085\sigma_{\mathrm{A}}{}^{2} + 0.009\sigma_{\mathrm{D}}{}^{2} \quad (8)$$

Variance components can be calculated by equations (1) and (2), using Cov (FS) (equation (3)), Cov (HS) (equation (4)), Cov (FS) (equations (5) and (6)) and Cov (HS) (equations (7) and (8)).

However, 2x + 1 pollen could also fertilize in artificial autotetraploid *Astragalus sinicus* L. as reported by Hayashi and Kiwata[14)]. To evaluate the contribution of 2x + 1 pollens to the covariance of a population, covariances were calculated for a case where fertilization with both 2x and 2x + 1 pollen was possible, under the same condition. 2x + 1 pollen results from a 1-3 and 2-3 disjunction of a quadrivalent and pentavalent chromosome, and the probabilities of such types of disjunction are defined as $\lambda = 0.2$ $(= 1-\kappa)$ and 1/2, respectively[21)]. The covariances of a population were calculated by applying the same method for the case where only 2x pollen could fertilize. The results are;

$$\mathrm{Cov}\ (\mathrm{FS})_{\mathrm{s}} = 0.235\mathrm{s}_{\mathrm{A}}{}^{2} + 0.115\mathrm{s}_{\mathrm{D}}{}^{2} + 0.050\mathrm{s}_{\mathrm{T}}{}^{2} + 0.021\mathrm{s}_{\mathrm{F}}{}^{2} \quad (9)$$

$$\mathrm{Cov}\ (\mathrm{FS})_{\mathrm{d}} = 0.239\mathrm{s}_{\mathrm{A}}{}^{2} + 0.091\mathrm{s}_{\mathrm{D}}{}^{2} + 0.028\mathrm{s}_{\mathrm{T}}{}^{2} + 0.005\mathrm{s}_{\mathrm{F}}{}^{2} \quad (10)$$

$$\mathrm{Cov}\ (\mathrm{HS})_{\mathrm{s}} = 0.124\mathrm{s}_{\mathrm{A}}{}^{2} + 0.019\mathrm{s}_{\mathrm{D}}{}^{2} \quad (11)$$

$$\mathrm{Cov}\ (\mathrm{HS})_{\mathrm{d}} = 0.130\mathrm{s}_{\mathrm{A}}{}^{2} + 0.016\mathrm{s}_{\mathrm{D}}{}^{2} \quad (12)$$

Table 1 The ϕ, ψ, ϕ' and ψ'calculated for each combination of sib's critical chromosome number in 4x × 4x family (in case of fertilization by only 2x pollen)

Combinations	ϕ	ψ	ϕ'	ψ'
3 vs. 3	1.000	0.167	0.250	0.000
4 vs. 4	1.000	0.167	1.000	0.167
5 vs. 5	1.000	0.167	2.250	1.500

Table 2 Coefficients of variance components of full sib covariances with same chromosome numbers in 4x × 4x family (in case of fertilization by only 2x pollen)

Variance component	Combination of sib's critical chromosome number			
	3 vs. 3 $(\lambda^2/4)$*	4 vs. 4 (κ^2)	5 vs. 5 $(\lambda^2/4)$	mean
additive	0.417	0.500	0.650	0.331
digenic	0.139	0.222	0.392	0.147
trigenic	0.042	0.083	0.188	0.055
quadrigenic	0.000	0.028	0.050	0.018

* : Combination frequency in a family.

Discussion

The number of elements of the variance components are averaged in the covariance (3)～(12). Thus, these variance components can be interpreted as variance components with average constitution[21)].

Cov $(\mathrm{FS})_{\mathrm{aneu}}$ can be calculated by equations (5) and (6), and also by equations (9) and (10). Two values of Cov $(\mathrm{FS})_{\mathrm{aneu}}$ are different and the coefficients of additive genetic variance are different by 3.3%. The difference of the coefficients is 7.2% for Cov $(\mathrm{HS})_{\mathrm{aneu}}$. Hayashi and Kiwata[14)] reported that the fertilization ability of 2x + 1 pollen was 40% lower than that of 2x pollen in artificial autotetraploid in *Astragalus sinicus* L.. Taking this result and the probability of 3/8 into consideration, the frequencyof 2x + 1 pollen, which is responsible for a trait, proved to be only about 0.5% in *Astragalus sinicus* L.. Therefore, covariances calculated for the case where only 2x pollen fertilize can be used as reliable estimates for an artificial autotetraploid population of *Astragalus sinicus* L.. The coefficients of equations (5)～(8) may change according to κ. If κ is larger than 0.9, the coefficients of equations (5) and (6) will be nearly equal to the coefficient of equations (3), and also those of equations (7) and (8) will be nearly equal to those of equation (4). Therefore the analysis of variance is possible by using either Cov $(\mathrm{FS})_{\mathrm{eu}}$ and Cov $(\mathrm{HS})_{\mathrm{eu}}$ given by equations (3)-(4) or Cov $(\mathrm{FS})_{\mathrm{s}}$, Cov $(\mathrm{FS})_{\mathrm{d}}$, Cov $(\mathrm{HS})_{\mathrm{s}}$, and Cov $(\mathrm{HS})_{\mathrm{d}}$ given by equations (5)-(8), depending on experimental design.

In female gametes, fertilization ability may be different between euploid and aneuploid gametes. To examine the fertilization ability of female gametes in wheat, Kihara et al.[17)] examined the distribution of chromosome numbers in offspring derived from non-competitive crossing (*Triticum polonicum* x *T. spelta*) x (*Triticum polonicum* or *T. spelta*), (*Triticum durum* x *T. aestivum*) x (*Triticum durum* or *T. aestivum*). Other reports[14,29)] also indicated that the distributions of offspring chromosome numbers coincided with the assumption that all female gametes could equally fertilize. Based on these facts, it can be safely concluded that female gametes including euploid and aneuploid chromosome numbers have almost equal fertilization ability.

In the present study, it was assumed that every chromosome should be involved in aneuploidy with the same probability. However, the probability may be different between chromosomes. Therefore, for the accu-

Table 6 Coefficients of variance components of full sib covariances with same chromosome numbers in 4x ± a × 4x ± a families in case of fertilization by only 2x and 2x + 1 pollen (a = 0, 1)

Pollen parent	Seed parent			
	4x − 1 (0.094)*	4x (0.712)	4x + 1 (0.194)	mean
additive				
4x − 1 (0.094)*	0.306	0.386	0.290	0.360
4x (0.712)	0.234	0.216	0.255	0.225
4x + 1 (0.194)	0.209	0.177	0.343	0.212
mean	0.236	0.214	0.275	0.235
digenic				
4x − 1 (0.094)	0.167	0.203	0.153	0.189
4x (0.712)	0.111	0.107	0.120	0.110
4x + 1 (0.194)	0.093	0.083	0.155	0.098
mean	0.113	0.111	0.130	0.115
trigenic				
4x − 1 (0.094)	0.083	0.093	0.070	0.088
4x (0.712)	0.049	0.047	0.049	0.048
4x + 1 (0.194)	0.045	0.036	0.063	0.041
mean	0.051	0.049	0.054	0.050
quadrigenic				
4x − 1 (0.094)	0.028	0.037	0.021	0.033
4x (0.712)	0.017	0.014	0.047	0.021
4x + 1 (0.194)	0.012	0.011	0.020	0.013
mean	0.017	0.016	0.039	0.021

* : Frequency of individual in an equilibrium population

rate calculation of covariance of a population, the probability for each chromosome to be involved in aneuploidy should be evaluated by C-banding technique[2,3,9,11,34].

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Appendix

(I) Equation (9) is given in the following manner. Two and three alleles are inherited from 4x pollen as assumed, and thus the probabilities are p, r, and u for the pollen parent alleles. The number of alleles inherited from the seed parent is automatically settled by the number of alleles from the pollen, and thus the probabilities should be p, q, r, s, u, and v, all of which are equal to the pollen's probabilities. The combinations of same chromosome numbers are 5 vs. 5, 4 vs. 4, and 3 vs. 3 in a 4x × 4x family. As for the combination of 5 vs. 5, probabilities should be $p_{\text{pollen parent}} = 0.640$, $r_{\text{pollen parent}} = 0.160$, $u_{\text{pollen parent}} = 0.010$, $p_{\text{seed parent}} = 0.010$, $r_{\text{seed parent}} = 0.160$, and $u_{\text{seed parent}} = 0.640$ respectively, as shown in Table 3-(6) of Morisawa and Kato[21]. Therefore corrected probabilities should be $p_{\text{pollen parent}} = 0.790$, $r_{\text{pollen parent}} = 0.198$, $u_{\text{pollen parent}} = 0.012$, $p_{\text{seed parent}} = 0.012$, $r_{\text{seed parent}} = 0.198$, and $u_{\text{seed parent}} = 0.790$. The probabilities should be calculated for 4 vs. 4 and 3 vs. 3 in a similar manner. Based on these probabilities, the ϕ, ψ, ϕ', and ψ' can be calculated by using equations (3) and (6) of Morisawa and Kato[21], and the results are given in Table 4. The coefficients of the variance components for each combi-

Table 4 The ϕ, ψ, ϕ' and ψ' calculated for each combination of sib's critical chromosome number in 4x × 4x family (in case of fertilization by 2x and 2x + 1 pollen)

Combinations	ϕ	ψ	ϕ'	ψ'
3 vs. 3	1.000	0.167	0.250	0.000
4 vs. 4	1.114	0.249	0.892	0.132
5 vs. 5	1.114	0.249	2.087	1.286

Table 5 Coefficients of variance components of full sib covariances with same chromosome numbers in 4x × 4x family (in case of fertilization by 2x and 2x + 1 pollen)

Variance component	Combination of sib's critical chromosome number			
	3 vs. 3	4 vs. 4	5 vs. 5	mean
additive	0.417	0.502	0.640	0.216
digenic	0.139	0.229	0.386	0.107
trigenic	0.042	0.092	0.195	0.047
quadrigenic	0.000	0.033	0.064	0.014

nation can be obtained by equation (2), using the A, D, T, and Q in Table 1 of Morisawa and Kato[21)]. The results are given in Table 5. The coefficients of the variance components of the same chromosome number in 4x × 4x family can be calculated by the same maner as Table 2. The coefficients of variance components of other families are obtained in a similar maner. The results for each family are given in Table 6.

Therefore equation (9) is obtained as an average of these covariances, weighted by the frequency of each family in a population. Equations (10), (11), and (12) can be calculated similarly.

(II) The full and half sib family covariances with the same and different chromosome numbers can be calculated by equations (3) and (4), and by equations (5) to (8), respectively. The following simultaneous equations can be obtained by using probability v.

$$\begin{aligned}
\mathrm{Cov}\ (\mathrm{FS})_d &= (0.500-0.332v)\ S_A^2+(0.222\text{–}0.161v)\ S_D^2 \\
&\quad +(0.083-0.064v)\ S_T^2+(0.028-0.024v)\ S_F^2 \\
\mathrm{Cov}\ (\mathrm{HS})_s &= (0.250-0.098v)\ S_A^2+(0.028-0.009v)\ S_D^2 \\
\mathrm{Cov}\ (\mathrm{FS})_s-\mathrm{Cov}\ (\mathrm{FS})_d-\mathrm{Cov}\ (\mathrm{HS})_s &= \\
&= (-0.250-0.444v)\ S_A^2+(-0.028+0.086v) \\
&\quad S_D^2+(-0.034v)\ S_T^2+(0.016v)\ S_F^2 \\
\mathrm{Cov}\ (\mathrm{FS})_s &= (0.500-0.210v)\ S_A^2+(0.222-0.084v)\ S_D^2 \\
&\quad +(0.083-0.030v)\ S_T^2+(0.028-0.008v)\ S_F^2
\end{aligned}$$

The covariances will be obtained by the analysis of variance. Therefore, the strict solutions of these simultaneous equations will give genetic variances of a population. The detail of the analysis of variance will be reported elsewhere.

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異数体を含むレンゲ人為同質4倍体集団での全兄弟と半兄弟の共分散の計算

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任意交配するレンゲ人為同質4倍体集団における全兄弟と半兄弟の共分散を計算した．特定の相同染色体が必ずしも異数体に関わるとは限らないので，特定の相同染色体が関わる場合と関わらない場合について共分散を計算し，平均しなければならない．共分散を平均するため，特定の相同染色体が異数性に関わる確率を3/8とした“8”と“3”はゲノム染色体数と正4倍体で形成される4価染色体数の平均値である．

4価染色体は MI で確率$\kappa = 0.8$と$\lambda = 0.2$（$\kappa + \lambda = 1$）で2-2と1-3に分配され，Ⅲ価染色体とⅤ価染色体は確率1で1-2と2-3に分配されるとし，2xと2x+1花粉と雌性配偶子は等しく受精するとして共分散を計算した．両親の近交系数は$F = 0$であると仮定した．次いで家族の共分散を家族内の兄弟間の共分散の平均として計算し，集団の共分散を家族の共分散の平均として計算した．

仮定に基づき求めた共分散の分散成分の係数は2x花粉のみが受精するとして計算した値と違っていた．相加遺伝分散成分の係数は全兄弟と半兄弟でそれぞれ3.3%と7.2%ずつ違っていた．他の分散成分も同様であった．実際のレンゲ人為同質4倍体集団では2x+1花粉は受精能力が2x花粉より低く稀にしか受精しないので，2x花粉のみが受精するとして全兄弟と半兄弟の共分散を計算しても問題はないであろう．

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