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ON THE BIOMETRICAL GENETICS OF AUTOTETRAPLOID FROM A CROSS BETWEEN TWO PURE LINES

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Abstract

Killick (1971) considered some aspects of biometrical genetics of autotetraploids from a cross between two pure lines. By extending Tan and Chang (1972), in this paper we derive some general distribution results for autotetraploid populations from a cross between two pure lines. Using these distribution results, general formulas of genetic variances and covariances are then derived without assuming that double reduction does not exist. The present paper therefore extends some results given in Killick (1971), and in Mather and Jinks (1971) for disomic to tetrasomic populations.

Introduction

In a recent paper, Killick (1971) considered some aspects of biometrical genetics of autotetraploids from a cross between two pure lines. By extending Tan and Chang (1972), we derive in this paper some distribution theories of autotetraploid populations from a cross between two pure lines. These results are then used to derive general formulas for the genetic variances and covariances without assuming that double reduction does not exist. As in Killick (1971), we shall also restric ourselves to situations in which there are no genetic-environmental interactions, no selection, no linkage and no epistatic effects among loci, etc.. Moreover, it is assumed further that the errors are independently and identically distributed and that the effects of genes are equal over different loci. It is of interest to note that, with little modification, the formulas for the means, the variances and the covariances hold also without the assumption of equality of genotypic values from different loci.

In Section 2, some distribution theories are derived for segregating autotetraploid populations from a cross between two pure lines. These results are then used in Sections 3 and 4 to derive general formulas for genetic variances and covariances. These then extend results given in Hayman (1960), and Mather and Jinks (1971) to autotetraploid populations. For notations and terminologies, we shall basically follow (1971), Mather and Jinks (1971) and

Tan and Chang (1972), unless otherwise stated.

Some distribution theories of autotetraploid populations

We assume that there are n loci segregating independently and that there are only two alleles in each locus, say A_j and a_j for the jth locus. Then, as shown in the appendix, the frequencies at generation k ($k \geq 2$) of the genotypes ($a_j a_j a_j a_j$ (or $a_4^{(j)}$), $A_j a_j a_j a_j$ (or $A^{(j)} a_3^{(j)}$), $A_j A_j a_j a_j$ (or $A_2^{(j)} a_2^{(j)}$), $A_j A_j A_j a_j$ (or $A_3^{(j)} a^{(j)}$), $A_j A_j A_j A_j$ (or $(A_4^{(j)})$) are given by $\underset{\sim}{g}_{(k)}^{(3)} = (g_{1(k)}^{(3)}, g_{2(k)}^{(3)}, g_{3(k)}^{(3)}, g_{4(k)}^{(3)}, g_{5(k)}^{(3)})'$ as given in (a.5). Following Killick (1971), we let $(-d, h_1, h_2, h_3, d)$ denote the genotypic values of ($a_4^{(j)}$, $A^{(j)} a_3^{(j)}$, $A_2^{(j)} a_2^{(j)}$, $A_3^{(j)} a^{(j)}$, $A_4^{(j)}$). Then it is easily observed that the probability distribution of the genotypic value $G_{j(k)}$ of the jth locus for F_k is

$$\Pr\{G_{j(k)} = -d\} = g_{1(k)}^{(3)}, \ \Pr\{G_{j(k)} = h_{s-1}\} = g_{s(k)}^{(3)}, \ s=2,3,4,$$

and $\Pr\{G_{j(k)} = d\} = g_{5(k)}^{(3)}$; or, equivalently,

$$\begin{aligned} G_{j(k)} &= Z_{1(k)}^{(j)}(-d) + \sum_{s=2}^{4} Z_{s(k)}^{(j)} h_{s-1} + \Big(1 - \sum_{s=1}^{4} Z_{s(k)}^{(j)}\Big) d \\ &= -2d\, Z_{1(k)}^{(j)} + \sum_{s=2}^{4} (h_{s-1} - d) Z_{s(k)}^{(j)} + d, \end{aligned} \tag{2.1}$$

where $(Z_{1(k)}^{(j)}, Z_{2(k)}^{(j)}, Z_{3(k)}^{(j)}, Z_{4(k)}^{(j)}) = \underset{\sim}{Z}_{(k)}^{(j)\prime}$ is distributed as a four dimensional point multinomial $\underset{\sim}{Z}_{(k)}^{(j)} \sim \mathrm{Mult}\,(1;\ \underset{\sim}{g}_{(k)}^{(3)})$, using a notation of Tan and Chang (1972).

Let Y_k be the phenotypic value of F_k, $k \geq 2$. We have then for the representation of Y_k:

$$\begin{aligned} Y_k &= \mu_k + \sum_{j=1}^{n} G_{j(k)} + e_k \\ &= \mu_k - 2d \sum_{j=1}^{n} Z_{1(k)}^{(j)} + \sum_{s=2}^{4} (h_{s-1} - d) \Big(\sum_{j=1}^{n} Z_{s(k)}^{(j)} \Big) + nd + e_k \\ &= \mu_k - 2d\, Z_{1(k)} + \sum_{s=2}^{4} (h_{s-1} - d) Z_{s(k)} + nd + e_k, \end{aligned} \tag{2.2}$$

where μ_k is the grand mean of F_k and e_k the random disturbance (or enviro-nmental disturbance) associated with observing Y_k. Since $G_{j(k)}$ is independently and indentically distributed by assumption (no linkage and equality of effects), it is then easily verified that $\underset{\sim}{Z}_k' = (Z_{1(k)}, Z_{2(k)}, Z_{3(k)}, Z_{4(k)}) \sim \mathrm{Mult}\,(n;\ \underset{\sim}{g}_{(k)}^{(3)})$, a four dimensional multinomial distribution. Hence, if e_k is independently distributed as normal with mean 0 and variance σ_k^2, then, in the absence of genetic-enviro-nmental interactions, the probability density of Y_k can be written explicitly as

$$\begin{aligned} f_k(y) = \sum_{a_1=0}^{n} \sum_{a_2=0}^{n-a_1} \sum_{a_3=0}^{n-a_1-a_2} \sum_{a_4=0}^{n-a_1-a_2-a_3} \binom{n}{a_1, a_2, a_3, a_4} \prod_{j=1}^{5} (g_{j(k)}^{(3)})^{a_j} \frac{1}{\sqrt{2\pi}\,\sigma_k} \times \\ \exp\Big\{ -\frac{1}{2\sigma_k^2} \Big[y - \mu_k - nd + 2da_1 - \sum_{s=2}^{4} (h_{s-1} - d) a_s \Big]^2 \Big\}, \end{aligned} \tag{2.3}$$

where $a_5=n-a_1-a_2-a_3-a_4$ and $\binom{n}{a_1, a_2, a_3, a_4}=n!/(\Pi_{j=1}^{5}(a_j!))$.

Let $\underset{\sim}{f}^{(j)}$ be as given in the appendix, $j=2, 3, 4$. Then, it is seen that Y_k may also be represented by

$$
\begin{aligned}
Y_k=\mu_k+nd-2d\Big[&X_1^{(2)}+\sum_{j_1=2}^{4} X_{1(j_1)}^{(3)}+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4} X_{1(j_1j_2)}^{(4)} \\
&+\cdots+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{k-2}=2}^{4} X_{1(j_1j_2\cdots j_{k-2})}^{(k)}\Big] \\
&+\sum_{j=2}^{4}(h_{j-1}-d)\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{k-2}=2}^{4} X_{j(j_1j_2\cdots j_{k-2})}^{(k)}+e_k,
\end{aligned}
\tag{2.4}
$$

where

$$
\begin{aligned}
&\underset{\sim}{X}'_{(2)}=(X_1^{(2)}, X_2^{(2)}, X_3^{(2)}, X_4^{(2)}) \sim \mathrm{Mult}(n, \underset{\sim}{f}^{(3)}), \\
&\underset{\sim}{X}'_{(3)j_1}=(X_{1(j_1)}^{(3)}, X_{2(j_1)}^{(3)}, X_{3(j_1)}^{(3)}, X_{4(j_1)}^{(3)})\,|\,\underset{\sim}{X}_{(2)} \sim \mathrm{Mult}(X_{j_1}^{(2)}, \underset{\sim}{f}^{(j_1)}), \\
&\underset{\sim}{X}'_{(r)j_1j_2\cdots j_{r-2}}=(X_{1(j_1j_2\cdots j_{r-2})}^{(r)}, X_{2(j_1j_2\cdots j_{r-2})}^{(r)}, X_{3(j_1j_2\cdots j_{r-2})}^{(r)}, \\
&\quad X_{4(j_1j_2\cdots j_{r-2})}^{(r)})\,|\,\underset{\sim}{X}_{(r-1)j_1j_2\cdots j_{r-3}} \sim \mathrm{Mult}(X_{j_{r-2}(j_1j_2\cdots j_{r-3})}, \underset{\sim}{f}^{(j_{r-2})}), \\
&\quad r=4, \cdots, k, \quad j_1, j_2 \cdots j_{k-2}=2, 3, 4.
\end{aligned}
$$

It can readily be shown that (2.2) and (2.4) yield the same characteristic function (c. f. in short) $\psi_k(t)$ as

$$
\psi_k(t)=h_k(t)e^{it(\mu_k+nd)}\Big[g_{1(k)}^{(3)}e^{-2dit}+\sum_{j=2}^{4} g_{j(k)}^{(3)}e^{it(h_{j-1}-d)}+g_{5(k)}^{(3)}\Big]^n, \tag{2.5}
$$

where $i=\sqrt{-1}$ and $h_k(t)$ is the c. f. of e_k. It follows that the representations (2.2) and (2.4) are equivalent in the sense that they provide the same probability distribution. One may notice that $\underset{\sim}{X}_{(3)j_1}$ corresponds to the progenies in F_3 from the $A_{j_1-1}a_{5-j_1}$ F_2 individual and $\underset{\sim}{X}_{(4)j_1j_2}$ the progenies in F_4 from the $A_{j_2-1}a_{5-j_2}$ F_3 ancester and the $A_{j_1-1}a_{5-j_1}$ F_2 ancestor, etc.. In situations in which information about their ancestors is available, representation (2.4) may then enable us to implement this information into the analysis, as we shall see in the next two sections.

Some second degree statistics and their expectations

Using results given in the previous section, we derive in this section some second degree statistics for the tetrasomics without assuming that double reduction does not exist. This would provide analogous results in tetrasomics of the results given in Hayman (1960), Mather and Jinks (1971) and in Tan (1975) for disomics. We notice that, while our results are derived under the assumption of equality of genotypic values from different loci, the results for the means, the variances and the covariances hold also without making this assumption; in the latter case, one need only replace α, d, h_1, h_2, h_3 by α_j, d_j, h_{1j}, h_{2j}, h_{3j} and replace n by $\sum_j$, where α_j, d_j, h_{sj}, $s=1, 2, 3$ denote the quantities for the jth locus. For example, with the mean of $\mathbf{F}_k$ as given by $\mathcal{E}(\mathrm{Y}_k)=\mu_k+(n/(3(4-\alpha^2)))\times 4(1-\alpha)(1+2\alpha)(h_1+h_3)(\lambda_2^{k-1}-\lambda_3^{k-1})+nh_2/(4-\alpha^2)\ [(2-2\alpha+3\alpha^2)\lambda_2^{k-1}+2(1-\alpha)(1+2\alpha)\lambda_3^{k-1}]$ under the assumption of equality of genotypic values, the result without this assumption is then

$$\mathcal{E}(\mathrm{Y}_k)=\mu_k+\frac{4}{3}\sum_{j=1}^{n}\frac{1}{(4-\alpha_j^2)}(1-\alpha_j)(1+2\alpha_j)(h_{1j}+h_{3j})(\lambda_{2j}^{k-1}-\lambda_{3j}^{k-1})$$
$$+\sum_{j=1}^{n}\frac{1}{4-\alpha_j^2}h_{2j}[(2-2\alpha_j+3\alpha_j^2)\lambda_{2j}^{k-1}+2(1-\alpha_j)(1+2\alpha_j)\lambda_{3j}^{k-1}],$$

where $\lambda_1=(5-2\alpha)/6$, $\lambda_2=(1-\alpha)^2/6$, $\lambda_{2j}=(5-2\alpha_j)/6$ and $\lambda_{3j}=(1-\alpha_j)^2/6$.

Let $\mathrm{Y}_{ks_1s_2\cdots s_{k-1}}$ be the observed value of the s_{k-1}th $\mathbf{F}_k$ individual from the s_{k-2} th $\mathbf{F}_{k-1}$ ancestor, the s_{k-3}th $\mathbf{F}_{k-2}$ ancestor, …, the s_2th $\mathbf{F}_3$ ancestor and the s_1th $\mathbf{F}_2$ ancestor, and put

$$\bar{\mathrm{Y}}_{ks_1s_2\cdots s_{k-2}}=\frac{1}{m_{k-1}}\sum_{s_{k-1}=1}^{m_{k-1}}\mathrm{Y}_{ks_1s_2\cdots s_{k-1}},$$

$$\bar{\mathrm{Y}}_{ks_1s_2\cdots s_r\cdots}=\frac{1}{m_{r+1}}\sum_{s_{r+1}=1}^{m_{r+1}}\bar{\mathrm{Y}}_{ks_1s_2\cdots s_{r+1}\cdots},\quad r=1,2,\cdots k-3,$$

$\bar{\mathrm{Y}}_{k\cdots}=\dfrac{1}{m_1}\sum_{s_1=1}^{m_1}\bar{\mathrm{Y}}_{ks_1\cdots}$. For $k\geq 2$, define further $\mathrm{Var}(\bar{\mathrm{Y}}_{ks_1\cdots})=\mathrm{V}_{1\mathrm{F}_k}$,

$$\mathcal{E}\ \{\mathrm{Var}(\bar{\mathrm{Y}}_{ks_1s_2\cdots s_r\cdots}|s_1,s_2\cdots s_{r-1})\}=\mathrm{Y}_{r\mathrm{F}_k},\ r=2,3,\cdots k-1,$$

where $\mathrm{Var}(\bar{\mathrm{Y}}_{ks_1s_2\cdots s_r\cdots}|s_1,s_2\cdots s_{r-1})$ is the conditional variance of $\bar{\mathrm{Y}}_{ks_1s_2\cdots s_r\cdots}$ given $s_1,s_2\ldots s_{r-1}$.

Then $\mathrm{V}_{1\mathrm{F}_3}$, $\mathrm{V}_{2\mathrm{F}_3}$, $\mathrm{V}_{1\mathrm{F}_4}$, $\mathrm{V}_{2\mathrm{F}_4}$ and $\mathrm{V}_{3\mathrm{F}_4}$ are the variances as defined in Hayman (1960) and Mather and Jinks (1971) in the case of disomics; for general $k\geq 2$, $\mathrm{V}_{j\mathrm{F}_k}$, $j=1,2\cdots k-1$, have been given by Tan (1975) for disomics. By making use of the representation (2.4), in this section we shall proceed to find the explicit expression for $\mathrm{V}_{r\mathrm{F}_k}$ for tetrasomics without assuming that double reduction does not exist.

Now, using (2.4), we have for the representations of $\mathrm{Y}_{ks_1s_2\cdots s_{k-1}}$ and $\bar{\mathrm{Y}}_{ks_1s_2\cdots s_r\cdots}$, $r=1,2\cdots k-2$:

$$\mathrm{Y}_{ks_1s_2\cdots s_{k-1}}=\mu_k+nd-2d\Big[\mathrm{X}_{1;s_1}^{(2)}+\sum_{j_1=2}^{4}\mathrm{X}_{1(j_1);s_2(s_1)}^{(3)}+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}$$
$$\mathrm{X}_{1(j_1j_2);s_3(s_1s_2)}^{(4)}+\cdots+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{k-2}=2}^{4}\mathrm{X}_{1(j_1j_2\cdots j_{k-2});s_{k-1}(s_1s_2\cdots s_{k-2})}^{(k)}\Big]$$
$$+\sum_{j=2}^{4}(h_{j-1}-d)\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{k-2}=2}^{4}\mathrm{X}_{j(j_1j_2\cdots j_{k-2});s_{k-1}(s_1s_2\cdots s_{k-2})}^{(k)}$$
$$+e_{ks_1s_2\cdots s_{k-1}},\ s_j=1,2,\cdots m_j,\ j=1,2,\cdots k-1; \tag{3.1}$$

$$\bar{\mathrm{Y}}_{ks_1s_2\cdots s_r\cdots}=\mu_k+nd-2d\Big[\mathrm{X}_{1;s_1}^{(2)}+\sum_{j_1=2}^{4}\mathrm{X}_{1(j_1);s_2(s_1)}^{(3)}+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}$$
$$\mathrm{X}_{1(j_1j_2);s_3(s_1s_2)}^{(4)}+\cdots+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{r-1}=2}^{4}\mathrm{X}_{1(j_1j_2\cdots j_{r-1});s_r(s_1s_2\cdots s_{r-1})}^{(r+1)}\Big]$$

$$-2d\Big[\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_r=2}^{4}\bar{X}^{(r+2)}_{1(j_1j_2\cdots j_r);(s_1s_2\cdots s_r)}+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{r+1}=2}^{4}$$

$$\bar{X}^{(r+3)}_{1(j_1j_2\cdots j_{r+1});(s_1s_2\cdots s_r)}+\cdots+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{k-2}=2}^{4}\bar{X}^{(k)}_{1(j_1j_2\cdots j_{k-2});(s_1s_2\cdots s_r\cdots)}\Big]$$

$$+\sum_{j=2}^{4}(h_{j-1}-d)\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{k-2}=2}^{4}\bar{X}^{(k)}_{j(j_1j_2\cdots j_{k-2});(s_1s_2\cdots s_r\cdots)}$$

$$+\bar{e}_{ks_1s_2\cdots s_r\cdots}, \tag{3.2}$$

where

$$\bar{X}^{(l)}_{j(j_1j_2\cdots j_{l-2});(s_1s_2\cdots s_r\cdots)}=\frac{1}{m_{r+1}m_{r+2}\cdots m_{l-1}}\sum_{s_{r+1}=1}^{m_{r+1}}\sum_{s_{r+2}=1}^{m_{r+2}}\cdots\sum_{s_{l-1}=1}^{m_{l-1}}$$

$$X^{(l)}_{j(j_1j_2\cdots j_{l-2});s_{l-1}(s_1s_2\cdots s_l)},\qquad k\ge l\ge r+2,$$

$$\underset{\sim}{X}'_{(2);s_1}=(X^{(2)}_{1;s_1},\ X^{(2)}_{2;s_1},\ X^{(2)}_{3;s_1},\ X^{(2)}_{4;s_1})\sim\text{Mult}(n;\ f^{(3)}),\ s_1=1,2\cdots m_1,$$

independently,

$$\underset{\sim}{X}'_{(3)j_1;s_2(s_1)}=[X^{(3)}_{1(j_1);s_2(s_1)},\ X^{(3)}_{2(j_1);s_2(s_1)},\ X^{(3)}_{3(j_1);s_2(s_1)},\ X^{(3)}_{4(j_1);s_2(s_1)}]$$

$$|\underset{\sim}{X}_{(2);s_1}\sim\text{Mult}(X^{(2)}_{j_1;s_1},\ f^{(j_1)}),$$

independently for $s_2=1,2\cdots m_2$ for given s_1, and conditional on

$$\underset{\sim}{X}_{(r-1)j_1j_2\cdots j_{r-3};s_{r-2}(s_1s_2\cdots s_{r-3})},$$

$$\underset{\sim}{X}'_{(r)j_1j_2\cdots j_{r-2};s_{r-1}(s_1s_2\cdots s_{r-2})}=[X^{(r)}_{1(j_1j_2\cdots j_{r-2});s_{r-1}(s_1s_2\cdots s_{r-2})},$$

$$X^{(r)}_{2(j_1j_2\cdots j_{r-2});s_{r-1}(s_1s_2\cdots s_{r-2})},\ X^{(r)}_{3(j_1j_2\cdots j_{r-2});s_{r-1}(s_1s_2\cdots s_{r-2})},$$

$$X^{(r)}_{4(j_1j_2\cdots j_{r-2});s_{r-1}(s_1s_2\cdots s_{r-2})}]\,|\,\underset{\sim}{X}_{(r-1)j_1j_2\cdots j_{r-3};s_{r-2}(s_1s_2\cdots s_{r-3})}$$

$$\sim\text{Mult}(X^{(r-1)}_{j_{r-2}(j_1j_2\cdots j_{r-3});s_{r-2}(s_1s_2\cdots s_{r-3})};\ f^{(j_{r-2})}),$$

independently for $s_{r-1}=1,2\cdots m_{r-1}$ for given $s_1,s_2\cdots s_{r-2}$, $r=3,4,\cdots k$; furthermore, the $e_{ks_1s_2\cdots s_{k-1}}$'s are independently and identically distributed with mean 0 and variance σ_k^2, and also independently distributed of the random variables for genetic segregation.

(3.1) leads immediately to the c. f. of

$$Y_{ks_1s_2\cdots s_{k-1}}\text{ as }\psi_k(t)=e^{it(\mu_k+nd)}h_k(t)\Big\{g^{(3)}_{1(k)}e^{-2dit}+\sum_{j=2}^{4}g^{(3)}_{j(k)}e^{it(h_{j-1}-d)}+g^{(3)}_5\Big\}^n$$

as given in (2.5). From this it follows that the expectation and variance of $Y_{ks_1s_2\cdots s_{k-1}}$ (and hence of F_k) are given respectively by

$$\mathcal{E}(Y_{ks_1s_2\cdots s_{k-1}})=\frac{1}{i}\Big\{\frac{d}{dt}\log\psi_k(t)\Big\}_{t=0}=\mu_k+nd+n\Big\{(-2d)g^{(3)}_{1(k)}$$

$$+\sum_{j=2}^{4}g^{(3)}_{j(k)}(h_{j-1}-d)\Big\}\text{ and }\operatorname{Var}(Y_{ks_1s_2\cdots s_{k-1}})=\frac{1}{i^2}\Big\{\frac{d^2}{dt^2}\log\psi_k(t)\Big\}_{t=0}$$

$$=\sigma_k^2+n\Big\{(2d)^2g^{(3)}_{1(k)}+\sum_{j=2}^{4}g^{(3)}_{j(k)}(h_{j-1}-d)^2-\Big[(-2d)g^{(3)}_{1(k)}$$

$$+\sum_{j=2}^{4}(h_{j-1}-d)g^{(3)}_{j(k)}\Big]^2\Big\}. \tag{3.3}$$

On substituting (a.5) into (3.3) and simplifying,

$$\mathcal{E}(Y_{ks_1s_2\cdots sk-1})=\mu_k+\frac{4}{3}n(h_1+h_3)q_3(\alpha)(\lambda_2^{k-1}-\lambda_3^{k-1})$$
$$+2nh_2[q_2(\alpha)\lambda_2^{k-1}+q_3(\alpha)\lambda_3^{k-1}], \tag{3.4}$$

and

$$V_{F_k}=\mathrm{Var}(Y_{ks_1s_2\cdots s_{k-1}})=\sigma_k^2+nd^2\left\{1-\frac{2}{3}q_1(\alpha)\lambda_2^{k-1}+\frac{2}{3}q_3(\alpha)\lambda_3^{k-1}\right\}$$
$$+\frac{4}{3}nq_3(\alpha)(\lambda_2^{k-1}-\lambda_3^{k-1})(h_1^2+h_3^2)+2nh_2^2(q_2(\alpha)\lambda_2^{k-1}+q_3(\alpha)\lambda_3^{k-1})$$
$$-n[2h_2(q_2(\alpha)\lambda_2^{k-1}+q_3(\alpha)\lambda_3^{k-1})+\frac{4}{3}(h_1+h_3)q_3(\alpha)(\lambda_2^{k-1}-\lambda_3^{k-1})]^2, \tag{3.5}$$

where $\lambda_2=(5-2\alpha)/6$, $\lambda_3=(1-\alpha)^2/6$, $q_1(\alpha)=(1/2(4-\alpha^2))(14+2\alpha-7\alpha^2)$, $q_2(\alpha)=(1/2(4-\alpha^2))(2-2\alpha+3\alpha^2)$ and $q_3(\alpha)=(1/(4-\alpha^2))(1-\alpha)(1+2\alpha)$, α being the fraction of double reduction. When $k=2$, V_{F_2} has been given in Killick (1971)(*).

For deriving the means and the variances of $\bar{Y}_{ks_1s_2\cdots s_r\cdots}$, we shall need the c. f. of $\bar{Y}_{ks_1s_2\cdots s_r\cdots}$. Put

$$Y_{ks_1s_2\cdots sk-1}=\bar{Y}_{ks_1sk-1},\ \Phi_{0j}^{(k)}(t)=e^{it(h_{j-1}-d)}$$

and

$$\Phi_{rj}^{(k)}(t)=\left\{f_1^{(j)}e^{-2dit/m_{k-r}}+\sum_{s=2}^{4}f_s^{(j)}\Phi_{(r-1)s}^{(k)}\left(\frac{t}{m_{k-r}}\right)+f_5^{(j)}\right\}^{m_{k-r}}, \tag{3.6}$$

$r=1,2\cdots$, $j=2,3,4$ and interpret $m_{r+1}\cdots m_{k-1}$ as 1 if $r=k-1$. Then, using (3.2), the c. f. $\Phi_r(t)$ of $\bar{Y}_{ks_1s_2\cdots s_r\cdots}$ can be derived readily as

$$\Phi_r(t)=e^{it(\mu_k+nd)}\left\{h_k\left(\frac{t}{m_{r+1}m_{r+2}\cdots m_{k-1}}\right)\right\}^{m_{r+1}m_{r+2}\cdots m_{k-1}}$$
$$\times g_{1(r+1)}^{(3)}e^{-2dit}+\sum_{j=2}^{4}g_{j(r+1)}^{(3)}\Phi_{(k-r-1)j}^{(k)}(t)+g_{5(r+1)}^{(3)}\Big\}^n,\ r=1,2\cdots k-1. \tag{3.7}$$

By taking derivatives we obtain then $\mathcal{E}(\bar{Y}_{ks_1s_2\cdots s_r\cdots})$ and $\mathrm{Var}(\bar{Y}_{ks_1s_2\cdots s_r\cdots})$ as

$$\mathcal{E}(\bar{Y}_{ks_1s_2\cdots s_r\cdots})=\frac{1}{i}\left(\frac{d}{dt}\log\phi_r(t)\right)_{t=0}=\mu_k+nd+n\Big\{-2dg_{1(r+1)}^{(3)}$$
$$+\sum_{j=2}^{4}g_{j(r+1)}^{(3)}\Delta_{(k-r-1)j}\Big\}$$

and

$$\mathrm{Var}(\bar{Y}_{ks_1s_2\cdots s_r\cdots})=\frac{1}{i^2}\left(\frac{d^2}{dt^2}\log\phi_r(t)\right)_{t=0}=\frac{\sigma_k^2}{m_{r+1}m_{r+2}\cdots m_{k-1}}$$
$$+n\Big\{\Big[(2d)^2g_{1(r+1)}^{(3)}+\sum_{j=2}^{4}g_{j(r+1)}^{(3)}L_{(k-r-1)j}^{(k)}\Big]-\Big[(-2d)g_{1(r+1)}^{(3)}$$
$$+\sum_{j=2}^{4}g_{j(r+1)}^{(3)}\times\Delta_{(k-r-1)j}\Big]^2\Big\}, \tag{3.8}$$

(*) There is a misprint in Killick (1971)'s formula; instead of -16, the coefficient of $(h_1h_2+h_2h_3)\alpha^4$ is 16.

where $\Delta_{rj}=(1/i)((d/dt)\Phi_{rj}^{(k)}(t))_{t=0}$ (Δ_{rj} is independent of k as proved in the appendix) and $L_{rj}^{(k)}=(1/i^2)((d^2/dt^2)\Phi_{rj}^{(k)}(t))_{t=0}$, $j=2,3,4$, $r=0,1,2,\cdots$. Given in Appendix (2), Δ_{rj} and $L_{rj}^{(k)}$ have been solved explicitly as functions of $\boldsymbol{\alpha}, d, h_1, h_2$ and h_3. Furthermore, it is shown in the appendix that

$$(-2d)g_{1(r+1)}^{(3)}+\sum_{j=2}^{4}g_{j(r+1)}^{(3)}\Delta_{(k-r-1)j}=(-2d)g_{1(k)}^{(3)}+\sum_{j=2}^{4}g_{j(k)}^{(3)}(h_{j-1}-d)$$
$$=\Delta_{(k-1)3} \text{ for all } r=0,1,2\cdots k-1 \text{ so that}$$
$$\mathcal{E}(\bar{Y}_{k\cdots})=\mathcal{E}(\bar{Y}_{ks_1s_2\cdots s_r\cdots})=\mathcal{E}(Y_{ks_1s_2\cdots s_{k-1}}) \text{ for all } r=1,2\cdots k-2.$$

For $r=1$, we have then

$$V_{1F_k}=\frac{\sigma_k^2}{m_2m_3\cdots m_{k-1}}+n\left\{\left[(2d)^2g_{1(2)}^{(3)}+\sum_{j=2}^{4}g_{j(2)}^{(3)}L_{(k-2)j}^{(k)}\right]-\Delta_{(k-1)3}^2\right\} \tag{3.9}$$

For deriving the expression for V_{rF_k}, $k-1\geq r\geq 2$, we notice that, by using (3.1) and (3.2), we have for the c. f. $\bar{Y}_{ks_1s_2\cdots s_r\cdots}$ given $s_1, s_2, \cdots s_{r-1}$:

$$\begin{aligned}\phi_r^{(*)}(t\,|\,s_1s_2\cdots s_{r-1})&=e^{it(\mu_k+nd)}\left\{h_k\left(\frac{t}{m_{r+1}m_{r+2}\cdots m_{k-1}}\right)\right\}^{m_{r+1}m_{r+2}\cdots m_{k-1}}\\&\times\exp\left\{(-2d)it\left[X_{1;s_1}^{(2)}+\sum_{j=2}^{4}X_{1(j_1);s_2(s_1)}^{(3)}+\cdots+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{r-2}=2}^{4}\right.\right.\\&\left.\left.\times X_{1(j_1j_2\cdots j_{r-2});s_{r-1}(s_1s_2s_{r-2})}^{(r)}\right]\right\}\prod_{j_1=2}^{4}\prod_{j_2=2}^{4}\cdots\prod_{j_{r-1}=2}^{4}\left\{f_1^{(j_{r-1})}e^{-2dit}\right.\\&\left.+\sum_{s=2}^{4}f_s^{(j_{r-1})}\Phi_{(k-r-1)s}^{(k)}(t)+f_5^{(j_{r-1})}\right\}X_{j_{r-1}(j_1j_2\cdots j_{r-2});s_{r-1}(s_1\cdots s_{r-2})}^{(r)}\end{aligned} \tag{3.10}$$

where $\bar{Y}_{ks_1s_2\cdots s_{k-1}}=Y_{ks_1s_2\cdots s_{k-1}}$ and $m_{r+1}m_{r+2}\cdots m_{k-1}$ is interpreted as 1 if $r=k-1$.

Using (3.10), the conditional mean and the conditional variance of $\bar{Y}_{ks_1s_2\cdots s_r\cdots}$ given $s_1, s_2, \cdots s_{r-1}$ are then obtained respectively as:

$$\begin{aligned}\mathcal{E}(\bar{Y}_{ks_1s_2\cdots s_r\cdots}\,|\,s_1,s_2,\cdots s_{r-1})&=\frac{1}{i}\left\{\frac{d}{dt}\log\phi_r^{(*)}(t\,|\,s_1,s_2,\cdots s_{r-1})\right\}_{t=0}\\&=\mu_k+nd-2d\left[X_{1;s_1}^{(2)}+\sum_{j_1=2}^{4}X_{1(j_1);s_2(s_1)}^{(3)}+\cdots+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{r-2}=2}^{4}\right.\\&\left.\quad X_{1(j_1j_2\cdots j_{r-2});s_{r-1}(s_1s_2\cdots s_{r-2})}^{(r)}\right]+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{r-1}=2}^{4}\\&\quad X_{j_{r-1}(j_1j_2\cdots j_{r-2});s_{r-1}(s_1s_2\cdots s_{r-2})}^{(r)}\left[(-2d)f_1^{(j_{r-1})}+\sum_{s=2}^{4}f_s^{(j_{r-1})}\Delta_{(k-r-1)s}\right],\end{aligned} \tag{3.11}$$

and

$$\begin{aligned}\mathrm{Var}(\bar{Y}_{ks_1s_2\cdots s_r\cdots}\,|\,s_1,s_2,\cdots s_{r-1})&=\frac{1}{i^2}\left\{\frac{d^2}{dt^2}\log\phi_r^{*}(t\,|\,s_1,s_2\cdots s_{r-1})\right\}_{t=0}\\&=\frac{\sigma_k^2}{m_{r+1}m_{r+2}\cdots m_{k-1}}+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{r-1}=2}^{4}X_{j_{r-1}(j_1j_2\cdots j_{r-2});s_{r-1}(s_1s_2\cdots s_{r-2})}^{(r)}\\&\quad\times\left[(2d)^2f_1^{(j_{r-1})}+\sum_{s=2}^{4}f_s^{(j_{r-1})}L_{(k-r-1)s}^{(k)}-\Delta_{(k-r)j_{r-1}}^2\right],\end{aligned} \tag{3.12}$$

Taking expectations and noting that $\mathcal{E}(X^{(2)}_{j;s_1})=nf^{(3)}_j$ for all $j=1,2,3,4,5$ and

$$\mathcal{E}(X^{(r)}_{j_{r-1}(j_1j_2\cdots j_{r-2});s_{r-1}(s_1s_2\cdots s_{r-2})})=f^{(j_{r-2})}_{j_{r-1}}X^{(r-1)}_{j_{r-2}(j_1j_2\cdots j_{r-3});s_{r-2}(s_1s_2\cdots s_{r-3})}$$

for all $r=3, 4, 5\cdots k$, $j_{r-1}=1, 2, 3, 4, 5$, $j_1, j_2\cdots j_{r-2}=2, 3, 4$, we obtain then:

$$\begin{aligned}
\mathcal{E}\{\mathcal{E}(\bar{Y}_{ks_1s_2\cdots s_r\cdots}|s_1, s_2, \cdots s_{r-1})\} &= \mu_k+nd-2dn\Big\{f^{(3)}_1+\sum_{j_1=2}^{4}f^{(3)}_{j_1}f^{(j_1)}_1 \\
&\quad +\cdots+\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{r-2}=2}^{4}f^{(3)}_{j_1}f^{(j_1)}_{j_2}f^{(j_2)}_{j_3}f^{(j_{r-2})}_1\Big\} \\
&\quad +n\sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{r-1}=2}^{4}f^{(3)}_{j_1}f^{(j_1)}_{j_2}f^{(j_2)}_{j_3}\cdots f^{(j_{r-2})}_{j_{r-1}}\Big[(-2d)f^{(j_{r-1})}_1+\sum_{s=2}^{4}f^{(j_{r-1})}_s\Delta_{(k-r-1)s}\Big] \\
&= \mu_k+nd-2dng^{(3)}_{1(r)}-2dn\sum_{s=2}^{4}g^{(3)}_{s(r)}f^{(s)}_1+n\sum_{s=2}^{4}g^{(3)}_{s(r+1)}\Delta_{(k-r-1)s} \\
&= \mu_k+nd+n\Big[(-2d)g^{(3)}_{1(r+1)}+\sum_{s=2}^{4}g^{(3)}_{s(r+1)}\Delta_{(k-r-1)s}\Big] \qquad (3.13)
\end{aligned}$$

$=\mathcal{E}(\bar{Y}_{ks_1\cdots s_r\cdots})=\mathcal{E}(\bar{Y}_{k\cdots})=\mathcal{E}(Y_{ks_1s_2\cdots s_{k-1}})=\Delta_{(k-1)3}$, and

$$\begin{aligned}
V_{rF_k} &= \mathcal{E}\{\mathrm{Var}(\bar{Y}_{ks_1s_2\cdots s_r\cdots}|s_1, s_2\cdots s_{r-1})\}=\frac{\sigma^2_k}{m_{r+1}m_{r+2}\cdots m_{k-1}} \\
&\quad +n\sum_{j=2}^{4}g^{(3)}_{j(r)}\Big[(2d)^2f^{(j)}_1+\sum_{s=2}^{4}f^{(j)}_sL^{(k)}_{(k-r-1)s}-\Delta^2_{(k-r)j}\Big] \\
&= \frac{\sigma^2_k}{m_{r+1}m_{r+2}\cdots m_{k-1}}+n\Big\{\Big[(2d)^2g^{(3)}_{1(r+1)}+\sum_{s=2}^{4}g^{(3)}_{s(r+1)}L^{(k)}_{(k-r-1)s}\Big] \\
&\quad -\Big[(2d)^2g^{(3)}_{1(r)}+\sum_{s=2}^{4}g^{(3)}_{s(r)}\Delta^2_{(k-r)s}\Big]\Big\},\ r=2, 3, \cdots k-1, \qquad (3.14)
\end{aligned}$$

where $m_{r+1}m_{r+2}\cdots m_{k-1}$ is taken to be 1 if $r=k-1$.

To conclude this section, we define

$$S_{1(k)}=\frac{1}{m_1}\sum_{s_1=1}^{m_1}(\bar{Y}_{ks_1\cdots}-\bar{Y}_{k\cdots})^2,$$

and

$$S_{r(k)}=\frac{1}{m_1m_2\cdots m_{r-1}(m_r-1)}\sum_{s_1=1}^{m_1}\sum_{s_2=1}^{m_2}\cdots\sum_{s_r=1}^{m_r}(\bar{Y}_{ks_1s_2\cdots s_r\cdots}-\bar{Y}_{ks_1s_2\cdots s_{r-1}\cdots})^2$$

$r=2, 3\cdots k-1$; then, we shall proceed to show that $\mathcal{E}(S_{r(k)})=V_{rF_k}$. Obviously $\mathcal{E}(S_{1(k)})=V_{1F_k}$. To show that $\mathcal{E}(S_{r(k)})=V_{rF_k}$, notice that

$$\mathcal{E}(\bar{Y}_{ks_1s_2\cdots s_r\cdots})=\mathcal{E}(\bar{Y}_{ks_1s_2\cdots s_{r-1}\cdots})$$

so that

$$\begin{aligned}
S_{r(k)} &= \frac{1}{m_1m_2\cdots m_{r-1}(m_r-1)}\sum_{s_1=1}^{m_1}\sum_{s_2=1}^{m_2}\cdots\sum_{s_{r-1}=1}^{m_{r-1}}\Big\{\sum_{s_r=1}^{m_r}(\bar{Y}_{ks_1s_2\cdots s_r\cdots} \\
&\quad -\mathcal{E}(\bar{Y}_{ks_1s_2\cdots s_r\cdots}))^2-m_r(\bar{Y}_{ks_1s_2\cdots s_{r-1}\cdots}-\mathcal{E}(\bar{Y}_{ks_1s_2\cdots s_{r-1}\cdots}))^2\Big\}.
\end{aligned}$$

It follows that

$$\mathcal{E}(S_{r(k)}) = \frac{m_r}{(m_r-1)}\{\mathrm{Var}(\bar{Y}_{ks_1s_2\cdots s_r\cdots}) - \mathrm{Var}(\bar{Y}_{ks_1s_2\cdots s_{r-1}\cdots})\}$$

$$= \frac{m_r}{(m_r-1)}\Big\{\Big(1-\frac{1}{m_r}\Big)\frac{\sigma_k^2}{m_{r+1}m_{r+2}\cdots m_{k-1}} + n\Big[(2d)^2 g^{(3)}_{1(r+1)} + \sum_{j=2}^{4} g^{(3)}_{j(r+1)} L^{(3)}_{(k-r-1)j}\Big] - n\Big[(2d)^2 g^{(3)}_{1(r)} + \sum_{j=2}^{4} g^{(3)}_{j(r)} L^{(k)}_{(k-r)j}\Big]\Big\}$$

On substituting

$$L^{(k)}_{(k-r)j} = \Big(1-\frac{1}{m_r}\Big)\Delta^2_{(k-r)j} + \frac{1}{m_r}(2d)^2 f_1^{(j)} + \frac{1}{m_r}\sum_{s=2}^{4} f_s^{(j)} L^{(k)}_{(k-r-1)s}$$

and simplifying, we have then

$$\mathcal{E}(S_{r(k)}) = \frac{\sigma_k^2}{m_{r+1}m_{r+2}\cdots m_{k-1}} + n\Big\{\Big[(2d)^2 g^{(3)}_{1(r+1)} + \sum_{j=2}^{4} g^{(3)}_{j(r+1)} L^{(k)}_{(k-r-1)j}\Big] - \Big[(2d)^2 g^{(3)}_{1(r)} + \sum_{j=2}^{4} g^{(3)}_{j(r)} \Delta^2_{(k-r)j}\Big]\Big\} = V_{rF_k},\ r=2,3,\cdots k-1.$$

The covariances between F_{k_1} and F_{k_2} for $k_2>k_1\geq 2$

Using the distribution results given in Section 2, one may also derive the covariances between the F_{k_1} and F_{k_2} ($k_2>k_1\geq 2$) phenotypic values. By making use of (3.1) (with k replacing k_1) and (3.2) (with k replacing k_2), we have in fact for the joint c. f. of $Y_{k_1s_1s_2\cdots s_{k_1-1}}$ and $\bar{Y}_{k_2s_1s_2\cdots s_{k_1-1}\cdots}$:

$$\psi(t_1,t_2) = \exp\{it_1(\mu_{k_1}+nd) + it_2(\mu_{k_2}+nd)\} h_{k_1}(t_1)\cdot \Big\{h_{k_2}\Big(\frac{t_2}{m_{k_1}m_{k_1+1}\cdots m_{k_2-1}}\Big)\Big\}^{m_{k_1}m_{k_1+1}\cdots m_{k_2-1}} \Big\{g^{(3)}_{1(k_1)} e^{-2di(t_1+t_2)} + \sum_{j=2}^{4} g^{(3)}_{j(k_1)} \Phi_{0j}(t_1)\Phi^{(k_2)}_{(k_2-k_1)j}(t_2) + g^{(3)}_{5(k_1)}\Big\}^n, \tag{4.1}$$

By taking derivative and simplifying, we obtain then the covariance $W_{F_{k_1}F_{k_2}}$ between $Y_{k_1s_1s_2\cdots s_{k_1-1}}$ and $\bar{Y}_{k_2s_1s_2\cdots s_{k_1-1}\cdots}$ as

$$W_{F_{k_1}F_{k_2}} = \frac{1}{i^2}\Big\{\frac{\partial^2}{\partial t_1\partial t_2}\log\psi(t_1,t_2)\Big\}_{t_1=t_2=0} \tag{4.2}$$

$$= n\{[(2d)^2 g^{(3)}_{1(k_1)} + \sum_{j=2}^{4} g^{(3)}_{j(k_1)}\Delta_{0j}\Delta_{(k_2-k_1)j}] - \Delta_{(k_1-1)3}\Delta_{(k_2-1)3}\}.$$

For $k_1\geq 3$, define now

$$W_{1F_{k_1k_2}} = \mathrm{Cov}(\bar{Y}_{k_1s_1\cdots}, \bar{Y}_{k_2s_1\cdots}),$$

$$W_{rF_{k_1k_2}} = \mathcal{E}\{\mathrm{Cov}(\bar{Y}_{k_1s_1\cdots s_r\cdots}, \bar{Y}_{k_2s_1\cdots s_r\cdots}|s_1,s_2\cdots s_{r-1})\},\ r=2,3,\cdots k_1-1,$$

and put

$$SP_{1(k_1,k_2)} = \frac{1}{m_1-1}\sum_{s_1=1}^{m_1}(\bar{Y}_{k_1s_1\cdots} - \bar{Y}_{k_1\cdots})(\bar{Y}_{k_2s_1\cdots} - \bar{Y}_{k_2\cdots}),$$

and

$$SP_{r(k_1,k_2)} = \frac{1}{m_1m_2\cdots m_{r-1}(m_r-1)}\sum_{s_1=1}^{m_1}\sum_{s_2=1}^{m_2}\cdots\sum_{s_r=1}^{m_r}(\bar{Y}_{k_1s_1\cdots s_r\cdots} - \bar{Y}_{k_1s_1s_2\cdots s_{r-1}\cdots}) \times (\bar{Y}_{k_2s_1\cdots s_r\cdots} - \bar{Y}_{k_2s_1\cdots s_{r-1}\cdots}),\ r=2,3,\cdots k_1-1.$$

In this section we shall proceed to find the explicit expression for $W_{rF_{k_1k_2}}$ and show that

$$\mathcal{E}(SP_{r(k_1,k_2)}) = W_{rF_{k_1k_2}} \quad \text{for} \quad r=1,2,\cdots k_1-1.$$

Put

$$\phi_{0j}(t_1,t_2) = \Phi_{0j}(t_1)\Phi^{(k2)}_{(k2-k1)j}(t_2), \tag{4.3}$$

$\phi_{rj}(t_1,t_2) = \{f_1^{(j)}e^{-2di(t_1+t_2)/m_{k_1-r}} + \sum_{s=2}^{4} f_s^{(j)}\phi_{(r-1)j}(t_1/(m_{k_1-r}),\ t_2/(m_{k_1-r})) + f_5^{(j)}\}^{m_{k_1-r}}$, $r=1,2,\cdots$, $j=2,3,4$, $\Phi_{0j}(t)=e^{it(h_{j-1}-d)}$ and $\Phi^{(k)}_{rj}(t)$ being given in (3.6). Then, as in Section 3, we have for the joint c. f. $\psi_r^{(*)}(t_1,t_2)$ of $\bar{Y}_{k_1s_1s_2\cdots s_r\cdots}$ and $\bar{Y}_{k_2s_1s_2\cdots s_r\cdots}$ and the conditional joint c. f. $\psi_r^{(*)}(t_1,t_2|s_1,s_2\cdots s_{r-1})$ of $\bar{Y}_{k_1s_1s_2\cdots s_r\cdots}$ and $\bar{Y}_{k_2s_1s_2\cdots s_r\cdots}$ given $s_1,s_2,\cdots s_{r-1}$:

$$\begin{aligned}\psi_r^{(*)}(t_1,t_2) &= \exp[it_1(\mu_{k_1}+nd)+it_2(\mu_{k_2}+nd)] \\ &\times \left\{h_{k_1}\left(\frac{t_1}{m_{r+1}m_{r+2}\cdots m_{k_1-1}}\right)\right\}^{m_{r+1}m_{r+2}\cdots m_{k_1-1}} \\ &\times \left\{h_{k_2}\left(\frac{t_2}{m_{r+1}m_{r+2}\cdots m_{k_2-1}}\right)\right\}^{m_{r+1}m_{r+2}\cdots m_{k_2-1}} \\ &\times \left\{g^{(3)}_{1(r+1)}e^{-2di(t_1+t_2)} + \sum_{s=2}^{4} g^{(3)}_{s(r+1)}\times\phi_{(k_1-r-1)s}(t_1,t_2) + g^{(3)}_{5(r+1)}\right\}^n,\end{aligned} \tag{4.4}$$

and

$$\begin{aligned}\psi_r^{(*)}(t_1,t_2|s_1,s_2\cdots s_{r-1}) &= \exp[it_1(\mu_{k_1}+nd)+it_2(\mu_{k_2}+nd)] \\ &\times \left\{h_{k_1}\left(\frac{t_1}{m_{r+1}m_{r+2}\cdots m_{k_1-1}}\right)\right\}^{m_{r+1}m_{r+2}\cdots m_{k_1-1}} \\ &\times \left\{h_{k_2}\left(\frac{t_2}{m_{r+1}m_{r+2}\cdots m_{k_2-1}}\right)\right\}^{m_{r+1}m_{r+2}\cdots m_{k_2-1}} \\ &\times \prod_{j_1=2}^{4}\prod_{j_2=2}^{4}\cdots\prod_{j_{r-1}=2}^{4}\left\{f_1^{(j_{r-1})}e^{-2di(t_1+t_2)} + \sum_{s=2}^{4} f_s^{(j_{r-1})}\phi_{(k_1-r-1)s}(t_1,t_2) + f_5^{(j_{r-1})}\right\} \\ &\times X^{(r)}_{j_{r-1}(j_1j_2\cdots j_{r-2});s_{r-1}(s_1s_2\cdots s_{r-2})},\end{aligned} \tag{4.5}$$

On taking derivatives and simplifying, we obtain the covariance $\mathrm{Cov}(\bar{Y}_{k_1s_1\cdots s_r\cdots}, \bar{Y}_{k_2s_1\cdots s_r\cdots})$ of $\bar{Y}_{k_1s_1s_2\cdots s_r\cdots}$ and $\bar{Y}_{k_2s_1s_2\cdots s_r\cdots}$ and the conditional covariance $\mathrm{Cov}(\bar{Y}_{k_1s_1s_2\cdots s_r\cdots}, \bar{Y}_{k_2s_1s_2\cdots s_r\cdots}|s_1,s_2,\cdots s_{r-1})$ of $\bar{Y}_{k_1s_1s_2\cdots s_r\cdots}$ and $\bar{Y}_{k_2s_1s_2\cdots s_r\cdots}$ given $s_1,s_2,\cdots s_{r-1}$ as:

$$\begin{aligned}\mathrm{Cov}(\bar{Y}_{k_1s_1s_2\cdots s_r\cdots}, \bar{Y}_{k_2s_1s_2\cdots s_r\cdots}) &= n\Big\{\Big[(2d)^2 g^{(3)}_{1(r+1)} \\ &+ \sum_{s=2}^{4} g^{(3)}_{s(r+1)}\Delta^{(*)}_{(k_1-r-1)s}\Big] - \Delta_{(k_1-1)3}\Delta_{(k_2-1)3},\end{aligned} \tag{4.6}$$

and

$$\begin{aligned}&\mathrm{Cov}(\bar{Y}_{k_1s_1s_2\cdots s_r\cdots}, \bar{Y}_{k_2s_1s_2\cdots s_r\cdots}|s_1,s_2,\cdots s_{r-1}) \\ &= \sum_{j_1=2}^{4}\sum_{j_2=2}^{4}\cdots\sum_{j_{r-1}=2}^{4} X^{(r)}_{j_{r-1}(j_1j_2\cdots j_{r-2});s_{r-1}(s_1s_2\cdots s_{r-2})}\Big\{\Big[(2d)^2 f_1^{(j_{r-1})} \\ &\quad + \sum_{s=2}^{4} f_s^{(j_{r-1})}\Delta^{(*)}_{(k_1-r-1)s}\Big] - \Delta_{(k_1-r)j_{r-1}}\Delta_{(k_2-r)j_{r-1}},\end{aligned} \tag{4.7}$$

where $\Delta_{rj}^{(*)}=(1/i^2)\{(\partial^2/\partial t_1\partial t_2)\phi_{rj}(t_1,t_2)\}_{t_1=t_2=0}$, $r=0,1,2\cdots$, $j=2,3,4$ have been given explicitly in Appendix (3).

From (4.6) and (4.7), we have then:

$$\begin{aligned}W_{1\mathrm{F}k_1k_2}&=\mathrm{Cov}(\bar{Y}_{k_1s_1\cdots},\ \bar{Y}_{k_2s_1\cdots})=n\Big\{\Big[(2d)^2g_{1(2)}^{(3)}+\sum_{s=2}^{4}g_{s(2)}^{(3)}\Delta_{(k_1-2)s}^{(*)}\Big]\\&\quad-\Delta_{(k_1-1)3}\Delta_{(k_2-1)3}\Big\}=n\Big\{f_1^{(3)}(2d)^2+\sum_{s=2}^{4}f_s^{(3)}\Delta^{*}_{(k_1-2)s}-\Delta_{(k_1-1)3}\Delta_{(k_2-1)s}\Big\},\end{aligned}\tag{4.8}$$

and

$$\begin{aligned}W_{r\mathrm{F}k_1k_2}&=\mathcal{E}\{\mathrm{Cov}(\bar{Y}_{k_1s_1s_2\cdots s_r\cdots},\ \bar{Y}_{k_2s_1s_2\cdots s_r\cdots}\,|\,s_1,s_2\cdots s_{r-1})\}\\&=n\Big\{\Big[(2d)^2g_{1(r+1)}^{(3)}+\sum_{s=2}^{4}g_{s(r+1)}^{(3)}\Delta_{(k_1-r-1)s}^{(*)}\Big]\\&\quad-\Big[(2d)^2g_{1(r)}^{(3)}+\sum_{s=2}^{4}g_{s(r)}^{(3)}\Delta_{(k_1-r)j}\Delta_{(k_2-r)j}\Big]\Big\},\end{aligned}\tag{4.9}$$

$r=2,3\cdots k_1-1$, with $\bar{Y}_{k_1s_1s_2\cdots sk_1-1}=Y_{k_1s_1s_2\cdots sk_1-1}$.

As in Section 3, it can similarly be shown that

$$\mathcal{E}\{SP_{r(k_1,k_2)}\}=W_{r\mathrm{F}k_1k_2},\ r=1,2\cdots k_1-1.$$

These results provide extensions of results given in Mather and Jinks to autotetraploid populations.

Discussion

In the analysis of biometrical genetics, usually the method of moments is used for estimating genetic parameters. Thus, the traditional approach as given in Mather and Jinks (1971) is to solve for the genetic parameters by solving the moment equations by using the ordinary least square or weighted least square methods. By introducing the probability distributions for quantitative traits, it is possible to introduce the maximum likelihood method (MLE in short) for estimating genetic parameters in quantitative characters. For diploid populations, some results are given in Tan and Chang (1972). By introducing the probability distributions for quantitative traits in autotetraploid populations, one may also extend the MLE method for estimating genetic parameters in biometrical genetics of tetrasomic populations, extending results in Tan and Chang (1972). The detailed analysis and procedure will be illustrated in another paper in which some simulated tetrasomic populations are generated for the analysis and for the comparisons between the moment method and the MLE method for estimating genetic parameters. In the present paper, we illustrate how the distribution theories can be used to derive the means, the variances and the covariances (in general, any order of moments or cumulants) as defined in Mather and Jinks (1971) in tetrasomic populations.

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Appendix

(1) Derivation of the genoptyic frequencies of F_k for $k\geq 2$. For deriving the genotypic frequencies of F_k, $k\geq 2$, we put $\underset{\sim}{f}^{(1)\prime}=(1,0,0,0,0)$, $\underset{\sim}{f}^{(5)\prime}=(0,0,0,0,1)$,

$$\underset{\sim}{f}^{(2)\prime}=\underset{\sim}{g}^{(2)\prime}_{(3)}=(f_1^{(2)}, \underset{\sim}{r}^{(2)\prime}_{(2)}, f_5^{(2)})=\Big(\frac{1}{16}(2+\alpha)^2,\ \frac{1}{4}(1-\alpha)(2+\alpha),\ \frac{1}{8}(2-2\alpha+3\alpha^2),\ \frac{1}{4}\alpha(1-\alpha),\ \frac{1}{16}\alpha^2\Big),$$

$$\underset{\sim}{f}^{(3)\prime}=\underset{\sim}{g}^{(3)\prime}_{(3)}=(f_1^{(3)}, \underset{\sim}{r}^{(3)\prime}_{(2)}, f_5^{(3)})=\Big(\frac{1}{36}(1+2\alpha)^2,\ \frac{2}{9}(1-\alpha)(1+2\alpha),\ \frac{1}{6}(3-4\alpha+4\alpha^2),\ \frac{2}{9}(1-\alpha)(1+2\alpha),\ \frac{1}{36}(1+2\alpha)^2\Big),$$

$$\underset{\sim}{f}^{(4)\prime}=\underset{\sim}{g}^{(4)\prime}_{(3)}=(f_1^{(4)}, \underset{\sim}{r}^{(4)\prime}_{(2)}, f_5^{(4)})=\Big(\frac{1}{16}\alpha^2,\ \frac{1}{4}\alpha(1-\alpha),\ \frac{1}{8}(2-2\alpha+3\alpha^2),\ \frac{1}{4}(1-\alpha)(2+\alpha),\ \frac{1}{16}(2+\alpha)^2\Big) \qquad \text{(a.1)}$$

and let $\underset{\sim}{g}^{(j)\prime}_{k+2}=\underset{\sim}{f}^{(j)\prime}F^k$, where α is the fraction of double reduction and F a 5×5 matrix whose jth row is $\underset{\sim}{f}^{(j)\prime}$, $j=1,2,3,4,5$. Then, as shown in Bennett (1968),

$\underset{\sim}{g}_k^{(3)\prime}=(g^{(3)}_{1(k)}, g^{(3)}_{2(k)}, g^{(3)}_{3(k)}, g^{(3)}_{4(k)}, g^{(3)}_{5(k)})=(g^{(3)}_{1(k)}, \underset{\sim}{r}^{(3)\prime}_{(k)}, g^{(3)}_{5(k)})$ is the frequency of $(a_4,\ Aa_3,\ A_2a_2,\ A_3a,\ A_4)$ in F_k, $k\geq 2$. For deriving $\underset{\sim}{g}_k^{(j)}$ explicitly, we put $\underset{\sim}{w}_1'=(f_1^{(2)}, f_1^{(3)}, f_1^{(4)})$, $\underset{\sim}{w}_2'=(f_5^{(2)}, f_5^{(3)}, f_5^{(4)})$, and $Q'=(r^{(2)}_{(2)}, r^{(3)}_{(2)}, r^{(4)}_{(2)})$. Then $Q^k=(\underset{\sim}{r}^{(2)}_{(2)}, \underset{\sim}{r}^{(3)}_{(2)}, \underset{\sim}{r}^{(4)}_{(2)})'Q^{k-1}$ and

$$F=\begin{pmatrix} 1 & \underset{\sim}{0}' & 0 \\ \underset{\sim}{w}_1 & Q & \underset{\sim}{w}_2 \\ 0 & \underset{\sim}{0}' & 1 \end{pmatrix}. \quad \text{Since} \quad F^k=\begin{pmatrix} 1 & \underset{\sim}{0}' & 0 \\ \sum_{j=0}^{k-1} Q^j \underset{\sim}{w}_1 & Q^k & \sum_{j=0}^{k-1} Q^j \underset{\sim}{w}_1 \\ 0 & \underset{\sim}{0}' & \phi \end{pmatrix}$$

and

$\underset{\sim}{g}^{(j)\prime}_{(k+1)}=\underset{\sim}{f}^{(j)\prime}F^{k-2}F=\underset{\sim}{g}^{(j)\prime}_{(k)}F$, so we have

$$g^{(j)}_{1(k+1)}=g^{(j)}_{1(k)}+\sum_{s=2}^{4}g^{(j)}_{s(k)}f^{(s)}_{1},\ g^{(j)}_{j_1(k+1)}=\sum_{s=2}^{4}g^{(j)}_{s(k)}f^{(s)}_{j_1},$$

$$j_1=2,3,4 \text{ and } g^{(j)}_{5(k+1)}=g^{(j)}_{5(k)}+\sum_{s=2}^{4}g^{(j)}_{s(k)}f^{(s)}_{5}, \tag{a.2}$$

Now, it is easily observed that Q has the spectral decomposition $Q=\sum_{s=1}^{3}\lambda_s E_s$, where $\lambda_1=(1/2)(1-\alpha)$, $\lambda_2=(1/6)(5-2\alpha)$ and $\lambda_3=(1/6)(1-\alpha)^2$ are the eigenvalues of Q, and

$$E_1=\begin{pmatrix}\frac{1}{2} & 0 & -\frac{1}{2}\\ 0 & 0 & 0\\ -\frac{1}{2} & 0 & \frac{1}{2}\end{pmatrix},$$

$$E_2=\frac{1}{4-\alpha^2}\begin{pmatrix}(1-\alpha)(1+2\alpha), & \frac{3}{4}(2-2\alpha+3\alpha^2), & (1-\alpha)(1+2\alpha)\\ \frac{4}{3}(1-\alpha)(1+2\alpha), & (2-2\alpha+3\alpha^2), & \frac{4}{3}(1-\alpha)(1+2\alpha)\\ (1-\alpha)(1+2\alpha), & \frac{3}{4}(2-2\alpha+3\alpha^2), & (1-\alpha)(1+2\alpha)\end{pmatrix} \text{ and}$$

$$E_3=\frac{1}{4-\alpha^2}\begin{pmatrix}\frac{1}{2}(2-2\alpha+3\alpha^2), & -\frac{3}{4}(2-2\alpha+3\alpha^2), & \frac{1}{2}(2-2\alpha+3\alpha^2)\\ -\frac{4}{3}(1-\alpha)(1+2\alpha), & 2(1-\alpha)(1+2\alpha), & -\frac{4}{3}(1-\alpha)(1+2\alpha)\\ \frac{1}{2}(2-2\alpha+3\alpha^2), & -\frac{3}{4}(2-2\alpha+3\alpha^2), & \frac{1}{2}(2-2\alpha+3\alpha^2)\end{pmatrix} \tag{a.3}$$

satisfying $\sum_{s=1}^{3}E_s=I_3$, $E_s^2=E_s$ and $E_sE_{s'}=0$ for $s\neq s'$. It follows that, for $k=1, 2, 3\cdots$,

$$(g^{(j)}_{1(k+1)}, \underset{\sim}{\gamma}^{(j)}_{(k+1)}, g^{(j)}_{5(k+1)})=\underset{\sim}{g}^{(j)\prime}_{(k+1)}=\underset{\sim}{f}^{(j)\prime}F^{k-1}=\Big(f^{(j)}_1+\sum_{s=0}^{k-2}\underset{\sim}{\gamma}^{(j)\prime}_{(2)}Q^s\underset{\sim}{w}_1,\ \underset{\sim}{\gamma}^{(j)\prime}_{(2)}Q^{k-1},$$
$$f^{(j)}_5+\sum_{s=0}^{k-2}\underset{\sim}{\gamma}^{(j)\prime}_{(2)}Q^s\underset{\sim}{w}_2\Big) \tag{a.4}$$

so that

$$g^{(j)}_{1(k+1)}=f^{(j)}_1+\sum_{u=1}^{3}\left(\frac{1-\lambda_u^{k-1}}{1-\lambda_u}\right)\underset{\sim}{\gamma}^{(j)\prime}_{(2)}E_u\underset{\sim}{w}_1,$$

$$g^{(j)}_{5(k+1)}=f^{(j)}_5+\sum_{u=1}^{3}\left(\frac{1-\lambda_u^{k-1}}{1-\lambda_u}\right)\underset{\sim}{\gamma}^{(j)\prime}_{(2)}E_u\underset{\sim}{w}_2,$$

and

$$\underset{\sim}{\gamma}^{(j)\prime}_{(k+1)}=(g^{(j)}_{2(k+1)}, g^{(j)}_{3(k+1)}, g^{(j)}_{4(k+1)})=\sum_{j=1}^{3}\lambda_u^{k-1}\underset{\sim}{\gamma}^{(j)\prime}_{(2)}E_u.$$

On substituting (a.1) and (a.3) into (a.4) and simplifying, we obtain:

$$\underset{\sim}{g}^{(2)\prime}_{(k)}=\Big[\frac{3}{4}-\frac{1}{4}(\lambda_1^{k-1}+q_1(\alpha)\lambda_2^{k-1}+q_2(\alpha)\lambda_3^{k-1}),\ \frac{1}{2}\lambda_1^{k-1}+q_2(\alpha)\lambda_3^{k-1}+q_3(\alpha)\lambda_2^{k-1},$$
$$\frac{3}{2}q_2(\alpha)(\lambda_2^{k-1}-\lambda_3^{k-1}),\ -\frac{1}{2}\lambda_1^{k-1}+q_3(\alpha)\lambda_2^{k-1}+q_2(\alpha)\lambda_3^{k-1},$$
$$\frac{1}{4}+\frac{1}{4}(\lambda_1^{k-1}-q_1(\alpha)\lambda_2^{k-1}-q_2(\alpha)\lambda_3^{k-1})\Big],$$

$$\underset{\sim}{g}^{(3)\prime}_{(k)}=\Big[\frac{1}{2}+\frac{1}{3}(q_3(\alpha)\lambda_3^{k-1}-q_1(\alpha)\lambda_2^{k-1}),\ \frac{4}{3}q_3(\alpha)(\lambda_2^{k-1}-\lambda_3^{k-1}),\ 2(q_2(\alpha)\lambda_2^{k-1}+q_3(\alpha)\lambda_3^{k-1}),$$
$$\frac{4}{3}q_3(\alpha)(\lambda_2^{k-1}-\lambda_3^{k-1}),\ \frac{1}{2}+\frac{1}{3}(q_3(\alpha)\lambda_3^{k-1}-q_1(\alpha)\lambda_2^{k-1})\Big], \tag{a.5}$$

and

$$\underset{\sim}{g}^{(4)\prime}_{(k)}=\Big[\frac{1}{4}+\frac{1}{4}(\lambda_1^{k-1}-q_1(\alpha)\lambda_2^{k-1}-q_2(\alpha)\lambda_3^{k-1}),\ -\frac{1}{2}\lambda_1^{k-1}+q_3(\alpha)\lambda_2^{k-1}+q_2(\alpha)\lambda_3^{k-1},$$
$$\frac{3}{2}q_2(\alpha)(\lambda_2^{k-1}-\lambda_3^{k-1}),\ \frac{1}{2}\lambda_1^{k}+q_3(\alpha)\lambda_2^{k-1}+q_2(\alpha)\lambda_3^{k-1},$$
$$\frac{3}{4}-\frac{1}{4}(\lambda_1^{k-1}+q_1(\alpha)\lambda_2^{k-1}+q_2(\alpha)\lambda_3^{k-1})\Big],$$

where

$$q_1(\alpha)=\frac{1}{2(4-\alpha^2)}(14+2\alpha-7\alpha^2),$$
$$q_2(\alpha)=\frac{1}{2(4-\alpha^2)}(2-2\alpha+3\alpha^2), \tag{a.6}$$

and

$$q_3(\alpha)=\frac{1}{(4-\alpha^2)}(1-\alpha)(1+2\alpha).$$

(2) Derivation of Δ_{rj} and $L^{(k)}_{rj}$, $j=2, 3, 4$, $r=0, 1, 2\cdots$. Since $\Phi^{(k)}_{0j}(t)=e^{it(h_{j-1}-d)}$, $j=2, 3, 4$, we have obviously $\Delta_{0j}=(h_{j-1}-d)$ and $L^{(k)}_{0j}=L_{0j}=(h_{j-1}-d)^2=\Delta^2_{0j}$ independent of k.

By taking derivatives, we obtain

$$\Delta_{rj}=\frac{1}{i}\left(\frac{d}{dt}\Phi^{(k)}_{rj}(t)\right)_{t=0}=(-2d)f_1^{(j)}+\sum_{s=2}^{4}f_s^{(j)}\Delta_{(r-1)s} \tag{a.7}$$

and

$$L^{(k)}_{rj}=\left(1-\frac{1}{m_{k-r}}\right)\Delta^2_{rj}+\frac{1}{m_{k-r}}(2d)^2f_1^{(j)}+\frac{1}{m_{k-r}}\sum_{s=2}^{4}f_s^{(j)}L^{(k)}_{(r-1)s}\,. \tag{a.8}$$

Putting $\underset{\sim}{\Delta}'_r=(\Delta_{r2}, \Delta_{r3}, \Delta_{r4})$,

$\underset{\sim}{L}^{(k)\prime}_r=(L^{(k)}_{r2}, L^{(k)}_{r3}, L^{(k)}_{r4})$, $\underset{\sim}{a}'_r=(\Delta^2_{r2}, \Delta^2_{r3}, \Delta^2_{r4})$

and $\underset{\sim}{b}_r=(2d)^2\underset{\sim}{w}_1-\underset{\sim}{a}_r$, (a.7) and (a.8) then lead to

$$\underset{\sim}{\Delta}_r=(-2d)(I_3+Q+Q^2+\cdots+Q^{r-1})\underset{\sim}{w}_1+Q^r\underset{\sim}{\Delta}_0$$
$$=(-2d)\sum_{u=1}^{3}\left(\frac{1-\lambda_u^r}{1-\lambda_u}\right)E_u\underset{\sim}{w}_1+\sum_{u=1}^{3}\lambda_u^rE_u\underset{\sim}{\Delta}_0, \tag{a.9}$$

and

$$\underset{\sim}{\mathrm{L}}_r^{(k)}=\underset{\sim}{a}_r+\sum_{j=1}^{r}\frac{1}{m_{k-r}m_{k-r+1}\cdots m_{k-r+j-1}}\mathrm{Q}^{j-1}(\underset{\sim}{b}_{r-j+1}+\mathrm{Q}\underset{\sim}{a}_{r-j})$$

$$=\underset{\sim}{a}_r+\sum_{u=1}^{3}\sum_{j=1}^{r}\frac{1}{m_{k-r}m_{k-r+1}\cdots m_{k-r+j-1}}\lambda_u^{j-1}\mathrm{E}_u(\underset{\sim}{b}_{r-j+1}+\lambda_u\underset{\sim}{a}_{r-j}), \quad \text{(a.10)}$$

$r=1, 2\cdots k.$

On substituing (a.3) and simplifying, we obtain then:

$$\Delta_{r2}=-d\left(\frac{3}{2}-\frac{1}{2}\lambda_1^r\right)+h_1\left(\frac{1}{2}\lambda_1^r+q_3(\alpha)\lambda_2^r+q_2(\alpha)\lambda_3^r\right)$$

$$+\frac{3}{2}h_2q_2(\alpha)(\lambda_2^r-\lambda_3^r)+h_3\left(-\frac{1}{2}\lambda_1^r+q_3(\alpha)\lambda_2^r+q_2(\alpha)\lambda_3^r\right), \quad \text{(a.11)}$$

$$\Delta_{r3}=-d+\frac{4}{3}(h_1+h_3)q_3(\alpha)(\lambda_2^r-\lambda_3^r)+2h_2(q_2(\alpha)\lambda_2^r+q_3(\alpha)\lambda_3^r),$$

$$\Delta_{r4}=-\frac{1}{2}d(1+\lambda_1^r)+h_1\left(-\frac{1}{2}\lambda_1^r+q_3(\alpha)\lambda_2^r+q_2(\alpha)\lambda_3^r\right)$$

$$+\frac{3}{2}h_2q_2(\alpha)(\lambda_2^r-\lambda_3^r)+h_3\left(\frac{1}{2}\lambda_1^r+q_3(\alpha)\lambda_2^r+q_2(\alpha)\lambda_3^r\right),$$

$$\underset{\sim}{\mathrm{L}}_r^{(k)}=\underset{\sim}{a}_r+\sum_{u=1}^{3}\sum_{j=1}^{r}\frac{1}{m_{k-r}m_{k-r+1}\cdots m_{k-r+j-1}}c_{uj}\lambda_u^{j-1}\underset{\sim}{e}_u,$$

where

$$\underset{\sim}{e}_1'=(1,0,-1),\ \underset{\sim}{e}_2'=(3,4,3),$$

$$\underset{\sim}{e}_3'=(3(2-2\alpha+3\alpha^2),\ -8(1-\alpha)(1+2\alpha),\ 3(2-2\alpha+3\alpha^2)),$$

$$c_{1j}=d^2(1+\alpha)+\frac{1}{2}(\lambda_1\Delta^2_{(r-j)2}-\lambda_1\Delta^2_{(r-j)4}-\Delta^2_{(r-j+1)2}+\Delta^2_{(r-j+1)4}),$$

$$c_{2j}=\frac{1}{18}d^2(1+2\alpha)q_1(\alpha)+\frac{1}{3}q_3(\alpha)(\lambda_2\Delta^2_{(r-j)2}+\lambda_2\Delta^2_{(r-j)4}-\Delta^2_{(r-j+1)2}-\Delta^2_{(r-j+1)4})$$

$$+\frac{1}{2}q_2(\alpha)(\lambda_2\Delta^2_{(r-j)3}-\Delta^2_{(r-j+1)3}). \quad \text{(a.12)}$$

and

$$c_{3j}=\frac{1}{36(4-\alpha^2)}d^2(5+2\alpha-\alpha^2)+\frac{1}{6(4-\alpha^2)}(\lambda_3\Delta^2_{(r-j)2}+\lambda_3\Delta^2_{(r-j)4}$$

$$-\Delta^2_{(r-j+1)2}-\Delta^2_{(r-j+1)4})+\frac{1}{4(4-\alpha^2)}(\Delta^2_{(r-j+1)3}-\lambda_3\Delta^2_{(r-j)3}),$$

with $q_1(\alpha)$, $q_2(\alpha)$ and $q_3(\alpha)$ being given in (a.5).

Notice that the Δ_{rj}'s are independent of k and the $\mathrm{L}_{rj}^{(k)}$'s depend on k only through m_{k-r}'s. Notice also that, by using (a.2) and (a.9), we have

$$(-2d)g^{(3)}_{1(r+1)}+\sum_{j=2}^{4}g^{(3)\prime}_{j(r+1)}\Delta_{(k-r-1)j}$$

$$=(-2d)\left\{f_1^{(3)}+\sum_{s=0}^{r-2}\underset{\sim}{r}_{(2)}^{(3)\prime}\mathrm{Q}^j\underset{\sim}{w}_1\right\}+\underset{\sim}{r}_{(2)}^{(3)\prime}\mathrm{Q}^{r-1}\underset{\sim}{\Delta}_{(k-r-1)}$$

$$=(-2d)\left\{f_1^{(3)}+\sum_{s=0}^{r-2}\underset{\sim}{r}_{(2)}^{(3)\prime}\mathrm{Q}^j\underset{\sim}{w}_1\right\}+\underset{\sim}{r}_{(2)}^{(3)\prime}\mathrm{Q}^{r-1}\{(-2d)(\mathrm{I}_3+\mathrm{Q}+\cdots+\mathrm{Q}^{k-r-2})\underset{\sim}{w}_1+\mathrm{Q}^{k-r-1}\underset{\sim}{\Delta}_0\}$$

$$=(-2d)\left\{f_1^{(3)}+\sum_{s=0}^{k-3}\underset{\sim}{r}_{(2)}^{(3)\prime}Q^j\underset{\sim}{w}_1\right\}+\underset{\sim}{r}_{(2)}^{(3)\prime}Q^{k-2}\underset{\sim}{\Delta}_0=\Delta_{(k-1)3}$$

$$=(-2d)g_{1(k)}^{(3)}+\sum_{j=2}^{4}g_{j(k)}^{(3)}\Delta_{0j},$$

for all $r=0,1,2,\cdots k-1$ with $\bar{Y}_{ks_1\cdots s_r\cdots}=\bar{Y}_{k\cdots}$ if $r=0$. It follows that $\mathcal{E}(\bar{Y}_{k\cdots})=\mathcal{E}(\bar{Y}_{ks_1s_2\cdots s_r\cdots})=\mathcal{E}(Y_{ks_1s_2\cdots s_{k-1}})$, for all $r=1,2,\cdots k-2$.

(3) Derivation of $\Delta_{rj}^{(*)}$, $r=0,1,2,\cdots$, $j=2,3,4$. Obviously, $\Delta_{0j}^{(*)}=\Delta_{0j}\Delta_{(k_2-k_1)j}$, $j=2,3,4$. Furthermore,

$$\left\{\frac{1}{i}\frac{\partial}{\partial t_1}\phi_{rj}(t_1,t_2)\right\}_{t_1=t_2=0}=\Delta_{rj} \tag{a.13}$$

and

$$\left\{\frac{1}{i}\frac{\partial}{\partial t_2}\phi_{rj}(t_1,t_2)\right\}_{t_1=t_2=0}=\Delta_{(k_2-k_1+r)j},\ j=2,3,4,\ r=0,1,2,\cdots.$$

On substituting (a.13) into

$$\Delta_{rj}^{(*)}=\frac{1}{i^2}\left\{\frac{\partial^2}{\partial t_1\partial t_2}\phi_{rj}(t_1,t_2)\right\}_{t_1=t_2=0},$$

we have:

$$\Delta_{rj}^{(*)}=\left(1-\frac{1}{m_{k_1-r}}\right)\Delta_{rj}\Delta_{(k_2-k_1+r)j}+\frac{1}{m_{k_1-r}}\left[(2d)^2f_1^{(j)}+\sum_{s=2}^{4}f_s^{(j)}\Delta_{(r-1)s}^{(*)}\right].$$

Or, putting $\underset{\sim}{\Delta}_r^{(*)}=(\Delta_{r2}^{(*)},\Delta_{r3}^{(*)},\Delta_{r4}^{(*)})'$,

$$\underset{\sim}{a}_r^{(*)}=(\Delta_{r2}\Delta_{(k_2-k_1+r)2},\ \Delta_{r3}\Delta_{(k_2-k_1+r)3},\ \Delta_{r4}\Delta_{(k_2-k_1+r)4})',$$

and

$$\underset{\sim}{b}_r^{(*)}=(2d)^2\underset{\sim}{w}_1-\underset{\sim}{a}_r^{(*)},$$

we have

$$\underset{\sim}{\Delta}_r^{(*)}=\underset{\sim}{a}_r^{(*)}+\frac{1}{m_{k_1-r}}(\underset{\sim}{b}_r^{(*)}+Q\underset{\sim}{\Delta}_{r-1}^{(*)}), \tag{a.14}$$

It follows that, for $r=1,2,\cdots$

$$\underset{\sim}{\Delta}_r^{(*)}=\underset{\sim}{a}_r^{(*)}+\sum_{j=1}^{r}\frac{1}{m_{k_1-r}m_{k_1-r+1}\cdots m_{k_1-r+j-1}}Q^{j-1}(\underset{\sim}{b}_{r-j+1}^{(*)}+Q\underset{\sim}{a}_{r-j}^{(*)})$$

$$=\underset{\sim}{a}_r^{(*)}+\sum_{u=1}^{3}\sum_{j=1}^{r}\frac{1}{m_{k_1-r}m_{k_1-r+1}\cdots m_{k_1-r+j-1}}\lambda_u^{j-1}E_u(\underset{\sim}{b}_{r-j+1}^{(*)}+\lambda_u\underset{\sim}{a}_{r-j}^{(*)})$$

Hence, as in the case of $\underset{\sim}{L}_r^{(k)}$, we have:

$$\underset{\sim}{\Delta}_r^{(*)}=\underset{\sim}{a}_r^{(*)}+\sum_{u=1}^{3}\sum_{j=1}^{r}\frac{1}{m_{k_1-r}m_{k_1-r+1}\cdots m_{k_1-r+j-1}}c_{uj}^{(*)}\lambda_u^{j-1}\underset{\sim}{e}_u, \tag{a.14}$$

where $\underset{\sim}{e}_u$, $u=1,2,3$, is given in (a.12) and $c_{uj}^{(*)}$ is derived from c_{uj} in (a.12) by replacing $\Delta_{(r-j)s}^2$ and $\Delta_{(r-j+1)s}^2$ by $\Delta_{(r-j)s}\Delta_{(k_2-k_1+r-j)s}$ and $\Delta_{(r-j+1)s}\Delta_{(k_2-k_1+r-j+1)s}$ respectively.

同原四元體的統計遺傳學研究

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本文係利用最大可能法探討兩純質同原四元體雜交後各世代的平均值，外表型與遺傳型變方以及其變積的一般化估算方法。