# Quantitative genetic analysis in *Phalaris tuberosa*

## I. THE STATISTICAL THEORY OF OPEN-POLLINATED PRGOENIES

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## 1. INTRODUCTION

In the analysis of quantitative variability in predominantly cross-fertilized forage species, it is often extremely convenient to make use of family groups produced by natural crossing. A group of offspring derived from a single ovule parent which has been pollinated under nursery conditions without control of male parentage, is commonly termed an open-pollinated progeny group. Single-cross families are those produced by controlled crossing of pairs of genotypes without emasculation. For the analysis of many traits it may be assumed that the offspring so derived represent half-sib and full-sib groups produced under random mating, provided the level of self-fertility in the species is sufficiently low; but for accurate analyses of seedling characters or of characters correlated with time of maturity, it may often be essential to consider the complexity introduced by maternal effects and by phenotypic assortative mating.

The present series of papers is concerned with the variation shown by date of ear emergence, seed weight, and measures of seedling growth rate in the Australian Commercial population of *Phalaris tuberosa* L. In this first communication, the statistical theory necessary for the interpretation of the available observations is developed: we will consider in turn the effects of partial self-fertilization, of phenotypic assortative mating, and of maternal effects, on the expectations of the observed covariances among relatives.

## 2. SELF-FERTILIZATION AND RANDOM MATING

The genetical structure of a population in equilibrium under a combination of self-fertilization and random mating has been studied by a number of authors. It was demonstrated by Haldane (1924) that if a proportion $s$ of all matings involve self-fertilization, the remainder being at random, equilibrium at an autosomal locus with two alleles $A_1$, $A_2$ implies that the genotype frequencies $f_{11}, f_{12}, f_{22}$ are such that

$$4f_{11}f_{22} - f_{12}^2 = \frac{s}{1-s}f_{12} \tag{1}$$

More recently, Bennett & Binet (1956) examined the approach to equilibrium of a pair of loci under this mating system, concluding that there exists a positive

association between the homozygous states at the two loci at equilibrium, even when the loci are located on different chromosomes. In both these studies it was assumed that all genotypes were equally viable. Hayman (1953) investigated the equilibrium conditions for a single locus at which natural selection favours the heterozygote at the expense of the two homozygotes.

The following model appears to be a little more realistic for the study of a quantitative character which is unaffected by natural selection, in a species which is predominantly out-breeding. Suppose each ovule parent gives rise to a proportion $s_i$ of inbred progeny and a proportion $1 - s_i$ of progeny produced by random mating, where $s_i$ varies independently of the level of homozygosity of the parental genotype and has mean $s$. Suppose further that the probability of survival of an inbred individual is $p$ relative to that of the outbred progeny, and let $k_i = ps_i/(1 - s_i + ps_i)$ denote the incidence of inbred individuals among the surviving members of a family, where $k_i$ has mean $k$ and variance $\sigma_k^2$.

Consider two unlinked loci with alleles $A_1, A_2$; $B_1, B_2$, with additive effects on the quantitative character under observation, and let $f_{11}^a, f_{12}^a, f_{22}^a; f_{11}^b, f_{12}^b, f_{22}^b$ denote the frequencies of the genotypes at each locus in the population of survivors. Then $f_1^a = f_{11}^a + \frac{1}{2}f_{12}^a, f_1^b = f_{11}^b + \frac{1}{2}f_{12}^b$, and $f_2^a = 1 - f_1^a, f_2^b = 1 - f_1^b$. At either locus, the change in $f_{11}$ in one generation is

$$\Delta(f_{11}) = \frac{ps(f_{12}) + (1 - s)(f_{12}^2 - 4f_{11}f_{22})}{4(1 - s + ps)}$$

so that at equilibrium

$$4f_{11}f_{22} - f_{12}^2 = \frac{ps}{1 - s}f_{12} \tag{2}$$

The theory of Bennett & Binet (1956) leads to the following equilibrium genotype frequencies in the population of survivors;

| Genotype | Frequency | Effect |
|---|---|---|
| $A_1 A_1 B_1 B_1$ | $f_{11}^a f_{11}^b + D$ | $-a - b$ |
| $A_1 A_1 B_1 B_2$ | $f_{11}^a f_{12}^b - 2D$ | $-a$ |
| $A_1 A_1 B_2 B_2$ | $f_{11}^a f_{22}^b + D$ | $-a + b$ |
| $A_1 A_2 B_1 B_1$ | $f_{12}^a f_{11}^b - 2D$ | $-b$ |
| $A_1 A_2 B_1 B_2$ | $f_{12}^a f_{12}^b + 4D$ | $0$ |
| $A_1 A_2 B_2 B_2$ | $f_{12}^a f_{22}^b - 2D$ | $+b$ |
| $A_2 A_2 B_1 B_1$ | $f_{22}^a f_{11}^b + D$ | $+a - b$ |
| $A_2 A_2 B_1 B_2$ | $f_{22}^a f_{12}^b - 2D$ | $+a$ |
| $A_2 A_2 B_2 B_2$ | $f_{22}^a f_{22}^b + D$ | $+a + b$ |

where

$$D = \frac{\frac{1}{4}ps(1 - s)(1 - s + ps)}{(1 - s + \frac{3}{4}ps)(1 - s + \frac{1}{2}ps)^2}f_1^a f_2^a f_1^b f_2^b$$

If we suppose the genotypic values to be as given in the third column above, the overall mean of the population is given by

$$\mu = a(f_2^a - f_1^a) + b(f_2^b - f_1^b),$$

and the total genetic variance is

$$\sigma_g^2 = 2a^2(f_1^a f_{22}^a + f_2^a f_{11}^a) + 2b^2(f_1^b f_{22}^b + f_2^b f_{11}^b)$$

which is the sum of the contributions of the individual loci.

Let $g_i$ denote the genotypic value of an ovule parent and $g_j$ that of a pollen parent, both expressed as deviations from the population mean: then the mean of their offspring will be $\frac{1}{2}(1-k_i)(g_i+g_j)+k_i g_i$, and the covariances of parent and offspring become

$$\mathrm{cov}\,(D, O) = E[\tfrac{1}{2}g_i^2(1+k_i)]$$
$$= \tfrac{1}{2}\sigma_g^2(1+k) \tag{3}$$
$$\mathrm{cov}\,(S, O) = E[\tfrac{1}{2}g_j^2(1-k_i)]$$
$$= \tfrac{1}{2}\sigma_g^2(1-k) \tag{4}$$

The covariance of mid-parent and offspring is therefore $\frac{1}{2}\sigma_g^2$.

The mean performance of the offspring of sire $(j)$ is obviously $\frac{1}{2}(1-k)g_j$, and the mean of the offspring of dam $(i)$ under open-pollination is similarly $\frac{1}{2}(1+k_i)g_i$. The component of variance among sires is therefore $\frac{1}{4}\sigma_g^2(1-k)^2$, and that among dams is $\frac{1}{4}\sigma_g^2[(1+k)^2+\sigma_k^2]$. The variance among single-cross family means is also readily shown to be $\frac{1}{2}\sigma_g^2(1+k^2+\sigma_k^2)$, so that an analysis of offspring performance can be expected to lead to the following partition of the total genetic variance:

| Source of variation | Component |
|---|---|
| Sires | $\frac{1}{4}\sigma_g^2(1-k)^2$ |
| Dams | $\frac{1}{4}\sigma_g^2[(1+k)^2+\sigma_k^2]$ |
| Sires × dams | $\frac{1}{4}\sigma_g^2(\sigma_k^2)$ |
| Within families | $\frac{1}{2}\sigma_g^2(1-k^2-\sigma_k^2)$ |
| Total | $\sigma_g^2$ |

## 3. THE CONSEQUENCES OF PHENOTYPIC ASSORTATIVE MATING

The foundations of the theory of phenotypic assortative mating were set out by Fisher (1918) and by Wright (1921). Reeve (1953, 1955, 1961) has studied in detail the estimation of heritability and genetic correlation in a progeny test involving assortative mating among parents taken from a random mating population, giving particular emphasis to the expectations of the regressions of offspring on mid-parent, and the components of variance and covariance among full-sib family groups. In the course of the analysis of the observations made of variation in ear emergence date and seed weight in *Phalaris tuberosa*, it has been necessary to derive corresponding formulae appropriate to half-sib families produced in a population in equilibrium under phenotypic assortative mating, and to consider the effects of genotype × season interaction on the estimation of genetic parameters under this mating system.

Expectations of the various covariances among relatives will be derived initially for a single additive genetic quantitative character which is not subject to

genotype × season interaction, so that the general method of approach can be outlined, and the notation introduced.

### (i) *A single additive genetic character under assortative mating*

The basic statistical theory involved in the derivation of expectations under phenotypic assortative mating may be set out in the following way. Suppose we are dealing with a sequence of ordered variables denoted by $X_i$, $i = 1, 2, \ldots n$, which show correlations $r_{ij}$, $i, j = 1, 2, \ldots n$: then the partial correlation coefficient $r_{ik.j}$ involving any three variables $X_i$, $X_j$ and $X_k$ taken in sequence, (i.e. $i < j < k$), is given by

$$r_{ik.j} = \frac{r_{ik} - r_{ij} r_{jk}}{(1 - r_{ij}^2)^{\frac{1}{2}} (1 - r_{jk}^2)^{\frac{1}{2}}}$$

In a model which specifies that all such $r_{ik.j}$ are equal to zero, it therefore follows that

$$r_{ik} = r_{ij} r_{jk} \qquad (5)$$

and the correlation between any pair of variables can then be expressed as the product of the correlations between all successive pairs of variables in the sequence. For example,

$$r_{14} = r_{13} r_{34} = r_{12} r_{23} r_{34}$$

Let $p$ be the phenotypic value of an individual and $g$ its breeding value, where $p$ is the sum of the breeding value and an independent environmental deviation, and suppose the observed assortative mating to be based on the measurement $p$ with correlation $\rho$. Suppose $p$ and $g$ to be measured as deviations from the population mean. If we consider the sequence of variables $g_i, p_i, p_j, g_j$, where subscripts $i$ and $j$ refer to female and male parameters respectively, the correlations between successive variables in the sequence are then $h, \rho, h$ respectively, where $h^2 = \sigma_g^2/\sigma_p^2$: the assumptions leading to equation (5) are clearly satisfied here, for if we hold the value of $p_i$ constant, the residual variation in $g_i$ is independent of that in $p_j$, and of that in $g_j$; similarly if the value of $p_j$ is held constant, the residual variation in $g_j$ is independent of that in $g_i$ and of that in $p_i$. The correlation between the breeding values of mates is therefore $\rho h^2$.

Since the mean performance of a group of offspring for an additive genetic character is $\frac{1}{2}(g_i + g_j)$, the covariance between ovule parent and offspring in a population in equilibrium is

$$\begin{aligned}
\text{cov}\,(D, O) &= \tfrac{1}{2} \text{cov}\,(p_i, g_i + g_j) \\
&= \tfrac{1}{2}(h + h\rho)\,\sigma_p\,\sigma_g \\
&= \tfrac{1}{2} h^2 (1 + \rho)\,\sigma_p^2
\end{aligned}$$

The expected mean of the open-pollinated progeny group derived from an ovule parent of breeding value $g_i$ and phenotypic value $p_i$ is given by the mean of $g_i$ and $E(g_j | p_i)$, the latter term denoting the mean value of $g_j$ in the relevant sub-population of pollen parents. It is easy to see that

$$E(g_j | p_i) = (\rho h^2) p_i$$

where $\rho h^2$ is the regression of $g_j$ on $p_i$: in a population in equilibrium under phenotypic assortative mating, the component of variance among half-sib group means is then equal to

$$\begin{aligned}
\mathrm{cov}\,(HS) &= \tfrac{1}{4}E(g_i + \rho h^2 p_i)^2 \\
&= \tfrac{1}{4}\sigma_g^2(1 + 2\rho h^2 + \rho^2 h^2) \\
&= \tfrac{1}{4}h^2[1 + \rho h^2(2 + \rho)]\,\sigma_p^2
\end{aligned}$$

The component of variance among full-sib group means is simply

$$\begin{aligned}
\mathrm{cov}\,(FS) &= \tfrac{1}{4}E(g_i + g_j)^2 \\
&= \tfrac{1}{4}(2\sigma_g^2 + 2\rho h^2\,\sigma_g^2) \\
&= \tfrac{1}{2}h^2(1 + \rho h^2)\,\sigma_p^2
\end{aligned}$$

(ii) *Two additive genetic characters subject to genotype × season interaction*

The following model has been found to be adequate for the present study of open-pollinated progeny groups in the Australian Commercial population of
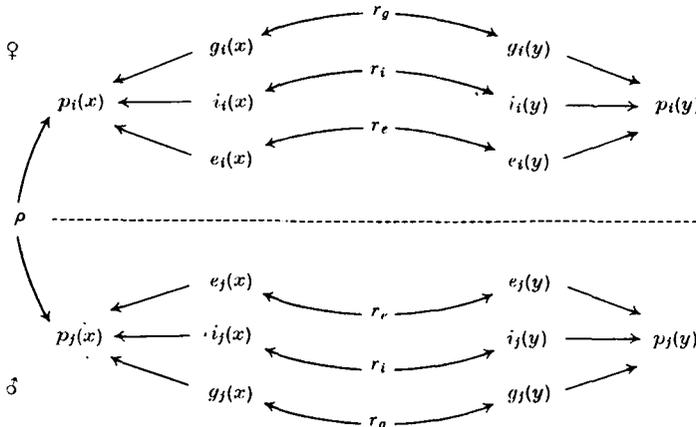


Fig. 1.    Statistical relationships among parameters of a pair of parents in the presence of phenotypic assortative mating.

*Phalaris.* Suppose characters $x$ and $y$ to show additive genetic variation in a population in equilibrium under phenotypic assortative mating of degree $\rho$ based on $p(x)$ and let

$$\begin{aligned}
p(x) &= g(x) + i(x) + e(x) \\
p(y) &= g(y) + i(y) + e(y)
\end{aligned}$$

i.e. suppose a phenotypic value to be the sum of a breeding value $g$, a genotype × season interaction effect $i$, and a within-season environmental deviation $e$, where $g$, $i$, and $e$ are uncorrelated and have zero means. Denote the correlation between $p(x)$ and $p(y)$ by $r_p$, and the corresponding correlations between breeding values, interaction effects and environmental deviations by $r_g$, $r_i$, and $r_e$. The usual assumptions that $g(x)$ is independent of $i(y)$ and of $e(y)$, and that $i(x)$ is independent of $e(y)$, etc., will also be made. The statistical relationships among these parameters for a pair of parents from the equilibrium population are illustrated in Fig. 1.

Consider firstly the expectations of the four possible parent–offspring covariances: let $h^2 = \sigma_g^2/\sigma_p^2$ as before, and let $i^2 = \sigma_i^2/\sigma_p^2$, and $e^2 = \sigma_e^2/\sigma_p^2$, so that $h^2 + i^2 + e^2 = 1$. The weighted mean breeding value for character $x$ of the pollen parents contributing to the open-pollinated progeny of an ovule parent of breeding value $g_i(x)$ and phenotypic value $p_i(x)$ is then

$$E[g_j(x)|\,p_i(x)] = \rho h^2(x)\,p_i(x)$$

and the covariance of ovule parent and offspring for character $x$ is therefore

$$
\begin{aligned}
\operatorname{cov}(D_x, O_x) &= \tfrac{1}{2}\operatorname{cov}[p_i(x), g_i(x) + \rho h^2(x)\,p_i(x)] \\
&= \tfrac{1}{2}[h(x)\,\sigma_p(x)\,\sigma_g(x) + \rho h^2(x)\,\sigma_p^2(x)] \\
&= \tfrac{1}{2}h^2(x)\,(1+\rho)\,\sigma_p^2(x)
\end{aligned}
\tag{6}
$$

By repeated application of equation (5), it can readily be shown that the weighted mean breeding value for character $y$ of the same set of pollen parents is

$$E[g_j(y)|\,p_i(x)] = \rho r_g\,\sigma_g(x)\,\sigma_g(y)\,p_i(x)/\sigma_p^2(x)$$

so that

$$
\begin{aligned}
\operatorname{cov}(D_x, O_y) &= \tfrac{1}{2}\operatorname{cov}[p_i(x), g_i(y) + \rho r_g\,\sigma_g(x)\,\sigma_g(y)\,p_i(x)/\sigma_p^2(x)] \\
&= \tfrac{1}{2}r_g\,\sigma_g(x)\,\sigma_g(y)\,(1+\rho) \\
&= \tfrac{1}{2}h(x)\,r_g\,h(y)\,(1+\rho)\,\sigma_p(x)\,\sigma_p(y)
\end{aligned}
\tag{7}
$$

In a similar manner, it can be seen that

$$
\begin{aligned}
\operatorname{cov}(D_y, O_x) &= \tfrac{1}{2}\operatorname{cov}[p_i(y), g_i(x) + \rho h^2(x)\,p_i(x)] \\
&= \tfrac{1}{2}[r_g\,h(y)\,\sigma_g(x)\,\sigma_p(y) + \rho h^2(x)\,r_p\,\sigma_p(x)\,\sigma_p(y)] \\
&= \tfrac{1}{2}[h(x)\,r_g\,h(y) + \rho h^2(x)\,r_p]\,\sigma_p(x)\,\sigma_p(y)
\end{aligned}
\tag{8}
$$

and the covariance of ovule parent and offspring for character $y$ is given by

$$
\begin{aligned}
\operatorname{cov}(D_y, O_y) &= \tfrac{1}{2}\operatorname{cov}[p_i(y), g_i(y) + \rho r_g\,\sigma_g(x)\,\sigma_g(y)\,p_i(x)/\sigma_p^2(x)] \\
&= \tfrac{1}{2}[h^2(y) + \rho h(x)\,r_g\,h(y)\,r_p]\,\sigma_p^2(y)
\end{aligned}
\tag{9}
$$

Expression (9) is most useful in that it specifies the bias involved in the estimation of the heritability of a character by means of the regression of offspring on ovule parent, when the effects of phenotypic assortative mating for flowering time are ignored. As one would expect, the estimate will be unbiased when the character under observation is genetically independent of time of maturity, whether or not the two characters be environmentally correlated. However, when a genetic relationship exists, the magnitude of the bias involved is a function of both the genetic correlation and the environmental correlation between the two variables.

Let us turn now to a consideration of the components of variance and covariance among progeny group means. The expected performance for character $x$ of an open-pollinated progeny group derived from an ovule parent with phenotypic value $p_i(x)$ and breeding value $g_i(x)$ is simply

$$\text{mean}\,(O_x) = \tfrac{1}{2}[g_i(x) + i'_i(x) + \rho h^2(x)\,p_i(x)]$$

where $i'_i(x)$ denotes the genotype $\times$ season interaction effect appropriate to the ovule parent genotype in the season during which the offspring generation is studied.

2B

The component of variance among progeny groups for character $x$ is then

$$\mathrm{cov}\,(HS_x) = \tfrac{1}{4}[\sigma_g^2(x) + \sigma_i^2(x) + \rho^2 h^4(x)\,\sigma_p^2(x) + 2\rho h^4(x)\,\sigma_p^2(x)]$$
$$= \tfrac{1}{4}[h_w^2(x) + \rho h^4(x)\,(2+\rho)]\,\sigma_p^2(x) \tag{10}$$

where $h_w^2(x)$ denotes the within-season heritability of character $x$. This expectation may also be derived by considering performance for the character in the parent season and that in the offspring season to be two distinct but genetically correlated variables.

The expected performance for character $y$ of the same open-pollinated progeny group is similarly given as

$$\mathrm{mean}\,(O_y) = \tfrac{1}{2}[g_i(y) + i_i'(y) + \rho r_g\,\sigma_g(x)\,\sigma_g(y)\,p_i(x)/\sigma_p^2(x)]$$

so that the component of variance among progeny groups for character $y$ is

$$\mathrm{cov}\,(HS_y) = \tfrac{1}{4}[\sigma_g^2(y) + \sigma_i^2(y) + \rho r_g^2 h^2(x)\,\sigma_g^2(y)\,(2+\rho)]$$
$$= \tfrac{1}{4}[h_w^2(y) + \rho(h(x)\,r_g\,h(y))^2\,(2+\rho)]\,\sigma_p^2(y) \tag{11}$$

The bias involved in estimating the within-season heritability for character $y$ from an analysis of open-pollinated progenies, when the effects of phenotypic assortative mating for character $x$ are ignored, can then be seen to depend on the genetic correlation between the two variables, but not on the environmental correlation. As we have seen, the magnitude of the corresponding bias in the parent–offspring estimate of heritability is a function of both the genetic and environmental correlations.

The expectation of the component of covariance among open-pollinated progeny groups for characters $x$ and $y$, can be derived from the above expressions for the group means of the two characters. It can be shown to be

$$\mathrm{cov}\,(HS_{xy}) = \tfrac{1}{4}[h_w(x)\,r_{g_w}\,h_w(y) + h^2(x)\,\rho(2+\rho)\,h(x)\,r_g\,h(y)]\,\sigma_p(x)\,\sigma_p(y) \tag{12}$$

where $r_{g_w}$ is the within-season genetic correlation between the two characters.

The expectations of the four possible parent–offspring covariances (expressions 6–9) can be seen to involve four parameters $\rho$, $h^2(x)$, $h^2(y)$, and $r_g$, apart from the phenotypic variances of the two characters and the phenotypic correlation between them, which can be estimated directly from the data. In theory it is therefore possible to obtain estimates of all four parameters from the observed covariances, but because of the complexity of the expectations, the errors of estimation involved can be anticipated to be quite high. If the assumptions of additivity of the genetic variances can be justified, however, it is possible to provide additional estimates of the parameters $h^2(x)$ and $h^2(y)$ if, as in the present study, one is dealing with a perennial species. These can be derived from observations of the repeatability of performance of individual plants in successive seasons. Equations 10, 11, and 12 can then be used to estimate $h_w^2(x)$, $h_w^2(y)$ and $r_{g_w}$, which, when compared with the corresponding estimates $h^2(x)$, $h^2(y)$ and $r_g$, give a measure of the contribution of genotype × season interaction to the variances of the two characters and to the correlation between them.

## 4. A MODEL FOR THE STUDY OF MATERNAL EFFECTS

Perhaps the most penetrating treatment of the theory of maternal effects in quantitative genetics is that of Kempthorne (1957), who considered a model involving an arbitrary degree of dominance as regards the direct effects, and also the genetically determined maternal effects, of the genotypes at a single autosomal locus. If one includes environmentally determined maternal effects, it turns out that nine parameters are involved in the expectations of the covariance of sire and offspring, the covariance of dam and offspring, the covariance among full-sibs, and the total phenotypic variance. It is therefore essential to use a less general model in the analysis of any set of experimental observations. For the study of variation in seedling growth-rate and of seed weight in *Phalaris tuberosa*, the following simplified model has been found to be adequate: in this paper we will merely set up the model and derive the necessary expectations, giving some attention to the type of information which has been considered in arriving at the simplifications involved.

Let $x$ denote the character subject to maternal influence (seedling growth rate), and let $y$ denote a measurable character related to maternal ability (for instance, a measure of the average size of seed produced by an individual plant). Suppose that the phenotypic value of an individual for character $x$ is the sum of an additive genetic value, a dominance effect, an additive genetic maternal effect, an environmental maternal effect, and an independent environmental deviation: i.e. that

$$p(x) = a(x) + d(x) + am(x) + em(x) + e(x)$$

Suppose also that the phenotypic value of the individual for character $y$ is simply the sum of an additive genetic value and an independent environmental deviation: i.e. that

$$p(y) = a(y) + e(y)$$

In the Australian Commercial population of *Phalaris tuberosa*, the parent–offspring correlation for seed weight has been found to be very high, and seed weight has been identified as the predominant factor in the determination of maternal ability. It has therefore been assumed above that the genetic variance shown by this character is additive, and that genetically determined maternal effects on seedling growth rate are also additive.

Consider a single autosomal locus with alleles $A_1$, $A_2$ making the following contributions to $p(x)$ and $p(y)$, where $am'(x)$ refers to the maternal effect of the gene common to a maternal half-sib group of offspring, and $a$, $b$, or $m$ may be negative, zero, or positive:

| | | *Effects on* | | |
|---|---|---|---|---|
| *Genotype* | *Frequency* | $a(x) + d(x)$ | $a(y)$ | $am'(x)$ |
| $A_1 A_1$ | $p^2$ | $-a$ | $-b$ | $-m$ |
| $A_1 A_2$ | $2pq$ | $d$ | $0$ | $0$ |
| $A_2 A_2$ | $q^2$ | $+a$ | $+b$ | $+m$ |

The covariance of a sire's performance for character $y$ and his offspring's performance for character $x$, which is the key observation upon which further simplification of the model rests, has expectation

$$\text{cov}\,(S_y, O_x) \;=\; \tfrac{1}{2}\,\text{cov}\,[a(x), a(y)] \tag{13}$$

since maternal effects are not involved here. If this covariance can be shown experimentally to be zero, and if character $y$ is the prime factor in the determination of inherited maternal ability, we may with little likelihood of error ignore the term $\text{cov}\,[a(x), am'(x)]$ in all the expectations which follow.

The covariance between a dam's performance for character $y$ and her offspring's performance for character $x$ is similarly expected to be

$$\text{cov}\,(D_y, O_x) \;=\; \tfrac{1}{2}\,\text{cov}\,[a(x), a(y)] + \text{cov}\,[am'(x), a(y)] + \text{cov}\,[em'(x), e(y)] \tag{14}$$

and the component of covariance between the two characters among maternal half-sib families has expectation

$$\begin{aligned}
\text{cov}\,(HS_{xy}) &= \text{cov}\,[\tfrac{1}{2}a(x) + am'(x) + em'(x), \tfrac{1}{2}a(y)] \\
&= \tfrac{1}{4}\,\text{cov}\,[a(x), a(y)] + \tfrac{1}{2}\,\text{cov}\,[am'(x), a(y)]
\end{aligned} \tag{15}$$

The phenotypic covariance between the two characters is expected to be

$$\begin{aligned}
\text{cov}\,[p(x), p(y)] &= \text{cov}\,[a(x), a(y)] + \text{cov}\,[e(x), e(y)] + \text{cov}\,[am(x), a(y)] \\
&\quad + \text{cov}\,[em(x), e(y)] \\
&= \text{cov}\,[a(x), a(y)] + \text{cov}\,[e(x), e(y)] + \tfrac{1}{2}\,\text{cov}\,[am'(x), a(y)]
\end{aligned} \tag{16}$$

since $\text{cov}\,[am(x), a(y)] = \tfrac{1}{2}\,\text{cov}\,[am'(x), a(y)]$, and $\text{cov}\,[em(x), e(y)] = 0$.

The expectations of the various covariances between relatives for character $x$ can be readily obtained from the treatment of Kempthorne (1957). The covariance of sire and offspring is

$$\begin{aligned}
\text{cov}\,(S_x, O_x) &= pq[a + d(p - q)]^2 + \tfrac{1}{2}pqm[a + d(p - q)] \\
&= \tfrac{1}{2}\sigma_a^2(x) + \tfrac{1}{4}\,\text{cov}\,[a(x), am'(x)]
\end{aligned} \tag{17}$$

and the covariance of dam and offspring (Fig. 2) is

$$\begin{aligned}
\text{cov}\,(D_x, O_x) &= pq[a + d(p - q)]^2 + pqm^2 + \tfrac{5}{2}pqm[a + d(p - q)] + \text{cov}\,[e(x), em'(x)] \\
&= \tfrac{1}{2}\sigma_a^2(x) + \tfrac{1}{2}\sigma_{am}^2(x) + \tfrac{5}{4}\,\text{cov}\,[a(x), am'(x)] + \text{cov}\,[e(x), em'(x)]
\end{aligned} \tag{18}$$

Note that the heritability of character $x$ should therefore be defined (Dickerson, 1947) as

$$h^2(x) \;=\; \frac{\sigma_a^2(x) + \tfrac{1}{2}\sigma_{am}^2(x) + \tfrac{3}{2}\,\text{cov}\,[a(x), am'(x)]}{\sigma_p^2(x)}$$

where

$$\sigma_p^2(x) \;=\; \sigma_a^2(x) + \sigma_d^2(x) + \sigma_{am}^2(x) + \sigma_{em}^2(x) + \sigma_e^2(x) + \text{cov}\,[a(x), am'(x)] \tag{19}$$

since $\text{cov}\,[a(x), am(x)] = \tfrac{1}{2}\,\text{cov}\,[a(x), am'(x)]$. Note that this definition of heritability includes only the *permanent* effects of the parents on the performance of their offspring, and the term $\text{cov}\,[e(x), em'(x)]$ which appears in the expectation of $\text{cov}\,(D_x, O_x)$ has not been included.

The covariance among full-sibs for character $x$ has been shown by Kempthorne to be

$$\text{cov}\,(FS_x) = \tfrac{1}{2}\sigma_a^2(x) + \tfrac{1}{4}\sigma_d^2(x) + \sigma_{am}^2(x) + \sigma_{em}^2(x) + \text{cov}\,[a(x), am'(x)] \qquad (20)$$

and the covariance among maternal half-sibs can readily be shown to have expectation

$$\begin{aligned}
\text{cov}\,(HS_x) &= E[\tfrac{1}{2}a(x) + am'(x) + em'(x)]^2 \\
&= \tfrac{1}{4}\sigma_a^2(x) + \sigma_{am}^2(x) + \sigma_{em}^2(x) + \text{cov}\,[a(x), am'(x)] \qquad (21)
\end{aligned}$$

The relationship between the two characters $x$ and $y$ can then be seen to involve four parameters which can in principle be estimated from the four expectations given (13–16). In the present study involving a perennial species, there is available an additional statistic designated $\text{cov}\,(D_y^*, O_x)$, which measures the covariance
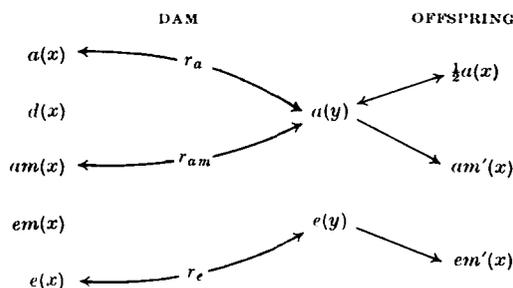


Fig. 2. Statistical relationships among parameters of ovule parent and offspring involving maternal effects of character $y$ on character $x$.

between the performance of an ovule parent for character $y$ in one season, and the performance for character $x$ of her offspring derived from seed harvested in a subsequent season. The expectation of this covariance is

$$\text{cov}\,(D_y^*, O_x) = \tfrac{1}{2}\text{cov}\,[a(x), a(y)] + \text{cov}\,[am'(x), a(y)] \qquad (22)$$

The corresponding statistic relating the performance of ovule parent and offspring for character $x$ has expectation

$$\text{cov}\,(D_x^*, O_x) = \tfrac{1}{2}\sigma_a^2(x) + \tfrac{1}{2}\sigma_{am}^2(x) + \tfrac{5}{4}\text{cov}\,[a(x), am'(x)] \qquad (23)$$

The six expressions (17–21, 23) involving character $x$ alone can be seen to involve seven parameters, so that a complete analysis is possible only when at least one parameter can justifiably be ignored. An unbiased estimate of the heritability of the character can however, be derived from expressions 17, 19 and 23.

## 5. DISCUSSION

The analysis of quantitative variability in the presence of a combination of self-fertilization and random mating, of phenotypic assortative mating, or of maternal effects, involves the use of somewhat complex expressions for the expectations of observed covariances among relatives. It is therefore to be anticipated that the errors of estimation of the basic parameters involved will be considerably

greater than those appropriate to estimates derived from more simple genetic models. The prime value of the theory which has been set out in this paper will therefore be in the *detection* of important sources of bias in an analysis which ignores the above phenomena. Having satisfied oneself that the biases involved are of a minor order, one may then choose to make use of the more accurate, though biased, estimates deriving from simpler theory. Where the effects of one or other of the potential sources of complexity can be shown to be of importance, however, one has no alternative but to apply the more elaborate theory.

In the analyses to be presented in subsequent papers in this series, it will be seen that the effects of phenotypic assortative mating and of maternal effects are of undeniable significance, though it has not been necessary to consider the simultaneous effects of these two phenomena in the analysis of any individual trait.

## SUMMARY

The present series of papers is concerned with the variation shown by date of ear emergence, seed weight, and measures of seedling growth rate in the Australian Commercial population of *Phalaris tuberosa* L. In this first communication, the statistical theory necessary for the interpretation of the available experimental observations is developed. The treatment involves a consideration of the effects of partial self-fertilization under open-pollination, of phenotypic assortative mating, and of maternal effects, on the expectations of the observed covariances among relatives.

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