

A BIOMETRICAL ANALYSIS OF MATROCLINOUS INHERITANCE OF GRAIN WEIGHT IN RICE

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1. INTRODUCTION

CYTOPLASMIC inheritance, as expressed in differences between reciprocal crosses, occurs extensively among cryptograms and angiosperms, and is associated with extreme oögamcy. Geneticists no longer consider hereditary transmission the total monopoly of the nucleus, but the mechanism of cytoplasmic inheritance is still imperfectly understood. Systems of self-propagating, extranuclear determinants or plasmagenes have been invoked by various workers (Darlington, 1939; Wright, 1941), but the possibility that, in certain instances, reciprocal differences between crosses result from the persistence in the cytoplasm of delayed nuclear effects must be conceded. The issue can be decided by an exchange of nuclei through repeated backcrossing to the male parent (Michaelis, 1954).

Striking reciprocal differences that derive from disturbances in the normal pattern of development have been the subject of much investigation. The quantitative and less spectacular expressions of matrocliny have received less attention. Quantitative matroclinous differences, however, are probably of greater significance in breeding, and possess the attraction of being more amenable to biometrical analysis. The instance of matroclinous inheritance of grain weight, which forms the subject of the biometrical analysis presented herein, was noted during the course of a study of the genetics of yield components in rice (*Oryza sativa* L.). The authors have been unable to find in the literature on the subject, a previous record of an attempt at the biometrical analysis of a character manifesting matroclinous inheritance.

2. MATERIALS AND METHODS

The rice pure lines *Vellai Ilankalayan 28061* (*v*) and *Panduruwi* (*p*) were used in reciprocal crosses made in 1949, at Peradeniya. Both varieties belong to the *indica* group of *Oryza sativa* L. *Vellai Ilankalayan 28061* possesses the coarse grain that characterises most varieties indigenous to Ceylon. *Panduruwi*, which is finer grained, is a selection within a variety of obscure antecedents, but probably of foreign origin. Progenies derived from these reciprocal crosses were grown in successive generations at the Central Rice Breeding Station, Batalagoda, and the weight of one hundred grains was recorded in hybrid populations and lines. In F_1 plants, the 100-grain weight was calculated from relatively small numbers. Table 1 indicates the numbers of plants and lines investigated in various generations.

3. GRAIN WEIGHT IN PARENTAL AND FILIAL GENERATIONS

Mean values of the 100-grain weight in parental varieties, reciprocal F_1 hybrids and segregating populations are given in table 1.

TABLE 1
100-grain weight in parents F_1 , F_2 and F_3

Generation	Notation	Number investigated	100-grain weight (gm.)
$P_1(p)$	x_0	96 plants	1.78
$P_2(v)$	y_0	31 "	3.02
$F_1(p \times v)$	x_1	5 "	2.02
$F_1(v \times p)$	y_1	8 "	2.47
$F_2(p \times v)$	{No. 25	74 "	} Average : 2.39
	{No. 31	15 "	
$F_2(v \times p)$	y_2	184 "	2.48
	{No. 25	13 lines	} Average : 2.37
{No. 31	6 "	2.38	

The 100-grain weights of the parents were 1.78 gm. and 3.02 gm., with a mid-parental value of 2.40 gm. The differences between reciprocal hybrids in both F_1 and F_2 generations indicate marked matrocliny: the 100-grain weights of $F_1(p \times v)$ and $F_1(v \times p)$ were 2.02 gm. and 2.47 gm. respectively. Reciprocal differences persisted in the F_2 generation: $F_2(v \times p)$ showed a higher value for the 100-grain weight than $F_2(p \times v)$. In the instance of the $p \times v$ cross at least, the maternal effect tended to decline in later generations. It is evident that in the crosses that form the subject of the present investigation, grain weight is controlled not only by nuclear genes but by cytoplasmic factors.

4. THE GENETIC MODEL

The following genetic model which has been constructed to fit the results presented above assumes that the phenotype of the hybrid is determined primarily by its genotype, but is affected by cytoplasmic

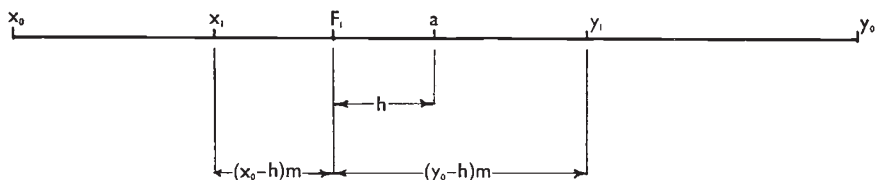


FIG. 1.—Genetic model of grain-weight inheritance in reciprocal hybrids: x_0 and y_0 are the parents, a is the midparental value, h is the deviation due to dominance, and m is a constant that provides a measure of the magnitude of the maternal effect.

factors contributed by the female parent. It is also assumed that the genotype of the female parent influences the nature of these cytoplasmic factors. Fig. 1 gives a diagram of the model.

On the basis of this model, the average phenotypic value of the various hybrid populations will be:

$$\left. \begin{aligned} x_1 &= a + h + \{(x_0 - a) - h\}m \\ x_2 &= a + \frac{h}{2} + \left\{ (x_1 - a) - \frac{h}{2} \right\} m \\ \vdots \\ x_n &= a + \frac{h}{2^{n-1}} + \left\{ (x_{n-1} - a) - \frac{h}{2^{n-1}} \right\} m \end{aligned} \right\} \quad (1)$$

and

$$\left. \begin{aligned} y_1 &= a + h + \{(y_0 - a) - h\}m \\ y_2 &= a + \frac{h}{2} + \left\{ (y_1 - a) - \frac{h}{2} \right\} m \\ \vdots \\ y_n &= a + \frac{h}{2^{n-1}} + \left\{ (y_{n-1} - a) - \frac{h}{2^{n-1}} \right\} m \end{aligned} \right\} \quad (2)$$

x_n and y_n can be re-written in the following form:

$$x_n = a(1-m) + \frac{h}{2^{n-1}} (1-m) + mx_{n-1} \quad (3)$$

and

$$y_n = a(1-m) + \frac{h}{2^{n-1}} (1-m) + my_{n-1} \quad (4)$$

The following two formulæ which are derived from (3) and (4) are functions of parental values:

$$x_n = a(1-m^n) + \frac{h(1-m)}{2^{n-1}} \frac{(1-2^{-nm^n})}{(1-2m)} + m^n x_0 \quad (5)$$

$$y_n = a(1-m^n) + \frac{h(1-m)}{2^{n-1}} \frac{(1-2^{-nm^n})}{(1-2m)} + m^n y_0 \quad (6)$$

substituting p for $a(1-m)$ and q for $h(1-m)$, the following equations for securing estimates of a , m and h are obtained.

$$\left. \begin{aligned} x_1 : p + q + 1.78m &= 2.02 \\ y_1 : p + q + 3.02m &= 2.47 \\ x_2 : p + 0.5q + 2.02m &= 2.39 \\ y_2 : p + 0.5q + 2.47m &= 2.48 \\ x_3 : p + 0.25q + 2.39m &= 2.37 \end{aligned} \right\} \quad (7)$$

The least squares method provides the following three simultaneous equations:

$$\left. \begin{aligned} 5p + 3.25q + 11.68m &= 11.73 \\ 3.25p + 2.5625q + 7.6425m &= 7.5175 \\ 11.68p + 7.6425q + 28.1822m &= 27.6727 \end{aligned} \right\} \quad (8)$$

The c -matrix obtained is

c_{pp}	-6.880052	c_{qp}	-1.159747	c_{mp}	-2.536908
c_{pq}	-1.159747	c_{qq}	2.236340	c_{mq}	-0.125802
c_{pm}	-2.536908	c_{qm}	-0.125802	c_{mm}	1.121010

Hence:

$$\left. \begin{aligned} m &= 0.3177 \pm 0.0710 \\ p &= a(1-m) = 1.7815 \pm 0.1759 \\ q &= h(1-m) = -0.2734 \pm 0.1003 \\ h &= -0.4008 \text{ and } a = 2.6111 \end{aligned} \right\} \quad (9)$$

and

Table 2 permits the comparison of observed values with expected values for different hybrid populations derived from the above estimates.

TABLE 2

Comparison of observed values with the expected values based on the genetic model

	Observed	Expected
x_1	2.02	2.0736
y_1	2.47	2.4675
x_2	2.39	2.3036
y_2	2.48	2.4288
x_3	2.37	2.4451

Comparison of observed and expected values in different hybrid populations in table 2 using the standard errors of estimated values demonstrates the adequacy of the genetic model.

5. PARTITIONING OF VARIANCE COMPONENTS IN HYBRID POPULATIONS

The methods and notation of Mather (1949) have been used in the partitioning of components of variation in various hybrid populations. The results are presented in table 3.

The observed variance and covariance values in different hybrid populations and the values expected on the basis of estimated D, H and E values described later are presented in table 4.

Equations for deriving estimates of D, H and E are as follows:

$$\left. \begin{aligned} E_1 &= 0.0072 \\ \frac{1}{2}(1-m)^2D + \frac{1}{4}(1-m)^2H + E_1 &= 0.0562 \\ \frac{1}{4}(1-m)^2D + \frac{1}{8}(1-m)^2H + E_1 &= 0.0247 \\ \frac{1}{2}(1-m)^2(1+m)^2D + \frac{1}{16}(1-m)^2(1+2m)^2H + E_2 &= 0.0415 \\ \frac{1}{8}(1-m)^2D + \frac{1}{16}(1-m)^2H + E_1 &= 0.0260 \\ \frac{1}{2}(1+m)(1-m)^2D + \frac{1}{8}(1+2m)(1-m)^2H &= 0.0332 \end{aligned} \right\} \quad (10)$$

Substituting 0.3177 for m (see (9)), and E_2 for $\frac{E_1}{n}$ (where $n = 42.20$, the harmonic mean of the number of individuals included in each F_3 line), we derive the following three simultaneous equations by the least squares method:

$$\left. \begin{aligned} 0.328532D + 0.096196H + 0.416921E_1 &= 0.044425 \\ 0.096196D + 0.032890H + 0.205515E_1 &= 0.015124 \\ 0.416921D + 0.205515H + 4.000562E_1 &= 0.115084 \end{aligned} \right\} \quad (11)$$

TABLE 3
Components of variation in various hybrid populations

	Notation	Components of variation
(1) Variance in parental varieties and reciprocal F ₁ hybrids	Vx ₀ , Vy ₀ , Vx ₁ , Vy ₁	E ₁
(2) Variance in F ₂	Vx ₂ , Vy ₂	$\frac{1}{2}(1-m)^2D$ + $\frac{1}{4}(1-m)^2H$ + E ₁
(3) Within-lines variance in F ₃	Vx ₃ (Wn), Vy ₃ (Wn)	$\frac{1}{4}(1-m)^2D$ + $\frac{1}{8}(1-m)^2H$ + E ₁
(4) Between-lines variance in F ₃	Vx̄ ₃ , Vȳ ₃	$\frac{1}{2}(1-m)^2(1+m)^2D$ + $\frac{1}{16}(1-m)^2(1+2m)^2H$ + E ₂
(5) Variance in bulked F ₃	Vx ₃ , Vy ₃	$\frac{1}{4}(1-m)^2(3+4m+2m^2)D$ + $\frac{1}{16}(1-m)^2(3+4m+4m^2)H$ + E ₁
(6) Within-lines variance in F ₄	Vx ₄ (Wn), Vy ₄ (Wn)	$\frac{1}{8}(1-m)^2D$ + $\frac{1}{16}(1-m)^2H$ + E ₁
(7) Variance in two backcrosses between F ₁ and P	VB(X)* + VB(Y)*	$\frac{1}{2}(1-m)^2D$ + $\frac{1}{2}(1-m)^2H$ + 2E ₁
(8) Covariance between F ₂ and F̄ ₃	Wx ₂ x̄ ₃ , Wy ₂ ȳ ₃	$\frac{1}{2}(1-m)^2(1+m)D$ + $\frac{1}{8}(1-m)^2(1+2m)H$
(9) Covariance between F ₃ and F̄ ₄	Wx ₃ x ₄ , Wy ₃ y ₄	$\frac{1}{4}(1+m)(1-m)^2(3+2m+2m^2)$ + $\frac{1}{32}(1-m)^2(3+8m+8m^2)H$

* Backcrosses fall into two groups, X and Y ; V_{B(X)} + V_{B(Y)} represents the sum of the variance of an X-group cross and the variance of a Y-group cross. The group X consists of backcrosses of F₁ to x₀ ; backcrosses to Y₀ compose group Y :

$$X \dots \begin{cases} x_0 \times y_1 \\ y_1 \times x_0 \\ x_1 \times x_0 \\ x_0 \times x_1 \end{cases} \quad Y \dots \begin{cases} y_0 \times y_1 \\ y_1 \times y_0 \\ x_1 \times y_0 \\ y_0 \times x_1 \end{cases}$$

TABLE 4
Observed and expected values of variance and covariance in parental varieties and hybrid populations

	Degrees of freedom	V or W	Pooled V or W	Expectation
Parents	$\begin{cases} Vx_0 & \cdot & \cdot & \cdot \\ Vy_0 & \cdot & \cdot & \cdot \end{cases}$	$\begin{matrix} 95 \\ 30 \end{matrix}$	$\begin{matrix} 0.0037 \\ 0.0159 \end{matrix}$	} 0.0072 0.0091
F ₁	$\begin{cases} Vx_1 & \cdot & \cdot & \cdot \\ Vy_1 & \cdot & \cdot & \cdot \end{cases}$	$\begin{matrix} 4 \\ 7 \end{matrix}$	$\begin{matrix} 0.0041 \\ 0.0192 \end{matrix}$	
F ₂	$\begin{cases} Vx_2 \text{ (No. 31)} & \cdot & \cdot & \cdot \\ Vx_2 \text{ (No. 25)} & \cdot & \cdot & \cdot \\ Vy_2 & \cdot & \cdot & \cdot \end{cases}$	$\begin{matrix} 14 \\ 73 \\ 183 \end{matrix}$	$\begin{matrix} 0.0268 \\ 0.0586 \\ 0.0575 \end{matrix}$	} 0.0562 0.0520
F ₃ (Wn)	$\begin{cases} Vx_3(Wn) \text{ (No. 25)} & \cdot & \cdot & \cdot \\ Vx_3(Wn) \text{ (No. 31)} & \cdot & \cdot & \cdot \end{cases}$	$\begin{matrix} 915 \\ 790 \end{matrix}$	$\begin{matrix} 0.0243 \\ 0.0252 \end{matrix}$	} 0.0247 0.0305
F ₃ (Bn)	$\begin{cases} Vx̄_3 \text{ (No. 25)} & \cdot & \cdot & \cdot \\ Vx̄_3 \text{ (No. 31)} & \cdot & \cdot & \cdot \end{cases}$	$\begin{matrix} 12 \\ 7 \end{matrix}$	$\begin{matrix} 0.0474 \\ 0.0314 \end{matrix}$	} 0.0415 0.0390
F ₄ (Wn)	$\begin{cases} Vx_4(Wn) \text{ (No. 25)} & \cdot & \cdot & \cdot \\ Vx_4(Wn) \text{ (No. 31)} & \cdot & \cdot & \cdot \end{cases}$	$\begin{matrix} 61 \\ 62 \end{matrix}$	$\begin{matrix} 0.0375 \\ 0.0147 \end{matrix}$	} 0.0260 0.0198
F ₂ /F ₃	$\begin{cases} Wx_2x_3 \text{ (No. 25)} & \cdot & \cdot & \cdot \\ Wx_2x_3 \text{ (No. 31)} & \cdot & \cdot & \cdot \end{cases}$	$\begin{matrix} 12 \\ 7 \end{matrix}$	$\begin{matrix} 0.0342 \\ 0.0314 \end{matrix}$	} 0.0332 0.0398

The c -matrix obtained is:

C_{DD}	27.673973	C_{HD}	-91.308962	C_{ED}	1.659270
C_{DH}	-91.308962	C_{HH}	344.385531	C_{EH}	-7.508961
C_{DE}	1.659270	C_{HE}	-7.508961	C_{EE}	0.425044

Estimated values D , H and E_1 are:

$$\left. \begin{aligned} D &= 0.0404 \pm 0.0392 \\ H &= 0.2879 \pm 0.1383 \\ E_1 &= 0.0091 \pm 0.0049 \end{aligned} \right\} \quad (12)$$

6. HERITABILITY

Components of variation in F_2 populations provide two estimates of heritability. The ratio of genetic variance to total variance measures heritability in the broad sense.

$$\frac{\frac{1}{2}(1-m)^2D + \frac{1}{4}(1-m)^2H}{\frac{1}{2}(1-m)^2D + \frac{1}{4}(1-m)^2H + E_1} = 0.7692 \quad (13)$$

Heritability in the narrow sense is defined as the ratio of additive genetic variance to total variance.

$$\frac{\frac{1}{2}(1-m)^2D}{\frac{1}{2}(1-m)^2D + \frac{1}{4}(1-m)^2H + E_1} = 0.4009 \quad (14)$$

The regression of F_3 lines on F_2 parents furnishes an estimate of heritability intermediate between the above two values.

$$b_{F_3/F_2} = \frac{W_{F_3/F_2}}{V_{F_2}} = 0.5907 \quad (15)$$

The correlation coefficient of F_2 individuals and F_3 lines is

$$r_{F_2/F_3} = \frac{W_{F_3/F_2}}{\sqrt{V_{F_2} \cdot V_{F_3}}} = 0.6874 \quad (16)$$

7. NUMBER OF EFFECTIVE FACTORS

The following calculation of the number of effective factors assumes (a) that all the genes have equal additive effects, and (b) that one parent carries all the plus allelomorphs and the other parent all the minus allelomorphs.

$$k = \frac{[\frac{1}{2}(\bar{P}_1 - \bar{P}_2)]^2}{D} = 9.51 \quad (17)$$

The number of effective factors is estimated to be about ten. It should, of course, be remembered that the assumptions implicit in the formula are unlikely to be completely justified.

8. DISCUSSION

A survey of the voluminous literature on cytoplasmic inheritance is not attempted in the following discussion: for reviews, reference may be made to Caspari (1948) and Michaelis (1954).

The results relating to matroclinous inheritance in the cross reported in this communication fit the hypothesis of extranuclear determinants transmitted to the hybrid through the cytoplasm of the female parent. The effect of these cytoplasm-borne determinants is to shift the phenotypic expression of the progeny towards that of the female parent. The direction of shift suggests that the maternal genotype influences the nature of the determinants.

The agreement between observed and expected values in tables 2 and 4 demonstrates the adequacy of the genetic model proposed in this paper.

The value of m , the coefficient of maternal effect, in grain-weight inheritance in the cross reported herein is 32 per cent. An investigation of matroclinous effects in a wide range of crosses would elucidate the nature of the cytoplasmic determinants involved.

The relation of the matroclinous inheritance of a character to its heritability is of considerable interest. Formulæ (13) and (14) show that the maternal effect depresses heritability. For instance, heritability in the narrow sense is given by the equation:

$$h^2 = \frac{\frac{1}{2}(1-m)^2D}{\frac{1}{2}(1-m)^2D + \frac{1}{4}(1-m)^2H + E_1} = \frac{\frac{1}{2}D}{\frac{1}{2}D + \frac{1}{4}H + E_1/(1-m)^2} \quad (18)$$

If m assumes a value between 1 and 0 (*i.e.* $1 > m > 0$), $\frac{E_1}{(1-m)^2}$ becomes larger than E_1 , and accordingly the value of h^2 falls.

If the maternal effect is complete, the heritability value will be zero exactly as in a homozygous line. An illustrative example in which D , H and E all assume the value of unity is given in table 5.

TABLE 5

The relation between maternal effect and heritability value

m	Heritability (per cent.)
0	28.6
0.1	25.2
0.2	21.6
0.3	17.9
0.4	14.2
0.5	10.5
0.6	7.1
0.7	4.2
0.8	1.9
0.9	0.5
1.0	0

It is noteworthy that if $E_1 = 0$, *i.e.* if the character under investigation is completely free of environmental variation, the maternal effect would not influence heritability.

The effect of matroclinous inheritance on the mean value of reciprocal-hybrid populations warrants consideration. Table 6 presents a computation of the difference in mean values of grain weight between the two reciprocal-hybrid populations, ($p \times v$) and ($v \times p$), over the generations F_1 to F_{10} . It will be noted that with successive selfings, the difference declines rapidly.

TABLE 6
Expected grain weights in reciprocal-hybrid populations

Filial generation	$h \times v$	$v \times h$	Difference
F_1	2.0736	2.4675	0.3939
F_2	2.3036	2.4288	0.1252
F_3	2.4451	2.4848	0.0397
F_4	2.5249	2.5375	0.0126
F_5	2.5674	2.5714	0.0040
F_6	2.5882	2.5896	0.0014
F_7	2.5959	2.5963	0.0004
F_8	2.6034	2.6035	0.0001
F_9	2.60819	2.60823	0.00004
F_{10}	2.60964	2.60966	0.00002

The genetical meaning of the following two formulæ may now be examined:

$$X_n = a(1-m^n) + \frac{h(1-m)}{2^{n-1}} \frac{(1-2^{-n}m^n)}{(1-2m)} + m^n x_0 \quad (5)$$

and

$$Y_n = a(1-m^n) + \frac{h(1-m)}{2^{n-1}} \frac{(1-2^{-n}m^n)}{(1-2m)} + m^n y_0 \quad (6)$$

In these two formulæ,

- if $m = 0$ (*i.e.* there is no maternal effect), then $X_n = Y_n = a + \frac{h}{2^{n-1}}$;
- if $m = 1$ (*i.e.* the maternal effect is complete), then in any hybrid generation, $X_n = X_0$ and $Y_n = Y_0$;
- if m assumes a value between 0 and 1 (*i.e.* $1 > m > 0$), the difference between reciprocal hybrid populations attributable to the maternal effect will decrease in successive generations (see table 6).

In the formulæ (5) and (6), if $n \rightarrow \infty$, then x_n and y_n approximate a . The difference between reciprocal hybrids is given by the equation,

$$y_n - x_n = m^n (y_0 - x_0) \quad (19)$$

In this equation, $m^n (y_0 - x_0)$ approaches zero if $n \rightarrow \infty$, because m has a value between 0 and 1.

9. SUMMARY

1. Grain weight in rice (*Oryza saliva* L.) has been found to exhibit matroclinous inheritance.

2. A genetic model has been constructed on the assumption that a system of extranuclear determinants can (a) interact with the genotype, (b) be transmitted to the progeny through the female cytoplasm, and (c) influence the phenotypic expression of the progeny for one generation.

3. Comparison of the experimental results with expected values computed on the basis of the above-mentioned assumption demonstrates the sufficiency of the hypothetical model.

4. Formulæ relating to grain weight in successive filial generations have been worked out, and components of variation have been partitioned by the methods of Mather (1949).

5. The value of m , the coefficient of maternal effect, is 32 per cent.

6. Heritability in the broad sense assumes a value of 0.77; heritability in the narrow sense has a value of 0.40.

7. The number of effective factors approximates ten.

8. The genetical meaning of matroclinous inheritance is discussed.

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