STUDIES ON THE QUANTITATIVE INHERITANCE
OF *ORYZA SATIVA*, L.

I.   A Diallel Analysis of Heading Time and Plant Height in F_1 Progeny[1]

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Introduction

A diallel cross is a set of p^2 possible single crosses and selfs between p homozygous (Hayman, 1954a, b, '58, '60) or heterozygous (Dickinson, 1956) parents; it provides a powerful method for investigating the relative genetical properties of these parents.   During the past few years there have appeared in the literatures several reports on the use of the diallel analysis in the study of quantitative characters of plants, such as flax (Durrant, 1964), tabacco (Hayman, 1954a; Jinks, 1954; Matzinger, 1962), maize (Matzinger, 1956; Hayman, 1958, '60), cotton (Hayman, 1958; Marani, 1963, '64; Miller, 1963; White, 1963, '64), alfalfa (Kehr, 1961; Theurer, 1963; Carnahan, 1963; Wilcox, 1964), winter wheat (Kronstad, 1964), spring wheat (Whitehouse, 1958), lima bean (Allard, 1956), soybean (Leffel, 1961), and tomato (Horner, 1957; Gilbert, 1958).   But until recently, none of such reports on the use of the diallel analysis in the study of quantitative inheritance of rice have been found.

In this paper, a study of basic nature on the quantitative inheritance of rice were carried out by means of diallel analysis with a view to estimating the genetic components and their standard errors from the second degree statistics, and to estimating such genetic parameters as additive, dominance and maternal effects, reciprocal difference, degree of dominance, allele frequency, heterosis and heritability of heading time and of plant height in F_1 progeny. Furthermore, it is expected that more information on the inheritance of these

two metric characters would be obtained in the early generations, and this kind of information will serve as a reference in the reassessment of the conventional breeding methodology.

Materials and Methods

The experimental materials consist of five parental varieties, namely, Yen-no (1), Wu-no-tao (2), Mang-hua-chu (3), Chih-chueh-chu (4), and Warisanmochi No. 2 (5). Crosses were made between these five varieties in accordance with a diallel scheme, including reciprocals and selfings. The 20 different F_1's together with the five parental varieties were planted in a completely randomized design, during the 1 st. crop season of 1966 at Nankang, Taipei.

All plants were recorded on an individual plant basis. The quantitative characters were evaluated as follows:

Heading time—recorded as number of days from the planting date to the date when the first panicle appears on the plant.

Plant height—measured to the centimeter at the maturity time before harvest.

The analysis of variance of the diallel table presented by Hayman (1954a) was used to estimate the variances of additive, dominance, and maternal effects.

The other statistics and the symbols used in this study are following Hayman (1954b):

1. The covariance between the p parents and their F_1 offspring in the rth array, (W_r).

2. The variance of the rth array, (V_r).

3. Variance of the parents, (V_p).

4. The mean value of W_r, $(\overline{W}_r)$.

5. The mean value of V_r, $(\overline{V}_r)$.

6. The variance of mean value of array, $(V_{\overline{r}})$.

7. The square of the difference between the mean of the parents and the mean of the F_1 progeny, $(\overline{P}-\overline{F}_1)^2=\frac{1}{4}\delta^2$.

These statistics were used in estimating the genetic components: D, H_1, H_2, F, and δ^2, whereby the following genetic parameters were further estimated.

1. An overall measure of the degree of dominance, $(H_1/D)^{1/2}$.

2. The mean value of the product of gene frequencies of dominance and recessive alleles, $\overline{uv}=(H_2/4H_1)$.

3. The ratio of the total numbers of dominant to recessive genes in all parents, $K_d/K_r=[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$,

4. An estimate of the number of groups of genes which control the character and exhibit dominance to some degree, $n=(\delta^2/H_2)$.

5. The order of dominance of the parents.

The heterosis of F_1 was estimated by the formula: $(\bar{F}_1-\bar{P}_0)/\bar{P}_0$, where $\bar{P}_0$ = the value of mid-parent. And the heritability of the matric character was estimated by the method of regression of the mean values of F_1 offspring on the value of mid-parent.

Results and Discussion

1. Analysis of diallel table

The results of the analysis of variance of the diallel table presented by Hayman (1954a) are given in Table 1.

Table 1. *Analysis of variance*

Source of variation	df	Heading time		Plant height	
		MS	F-value	MS	F-value
Treatment	24	61.3387	11.2755**	1,074.9820	16.3829**
(a)	4	84.6640	15.5632**	4,465.0240	68.0478**
(b)	10	57.5072	10.5712**	313.5072	4.7779**
(b_1)	1	307.3280	56.4941**	1,627.2080	24.7990**
(b_2)	4	58.4694	10.7481**	212.1827	3.2337*
(b_3)	5	6.7733	1.2451	131.8267	2.0091
(c)	4	119.3200	21.9338**	1,026.6600	15.6465**
(d)	6	13.5200	2.4853*	116.2933	1.7723
Error	100	5.4400		65.6160	
Total	124				

* and **: Significant at 5% and 1% level, respectively.

The interpretation of the results of Table 1 is straightforward. In both characters, the significance of (a) shows genetical variation amongst the parental varieties and that of (b), dominance at some of the loci; while that of (b_1) shows that the dominance is largely unidirection. The significance of (b_2) implies asymmetry in the gene distribution in both of these two characters. The other two items (c) and (d) shows that some maternal effect may be present in heading time, and may not be present in plant height.

2. Estimation of genetical components

The values of the various statistics estimated from the mean value of parental varieties and their progenies are shown in Table 2. (The values of V_r and W_r of each parental line were omitted.)

From the sign of δ of heading time (Table 2) we see that the progeny mean ($\bar{F}_1$) is less than the parental mean ($\bar{P}$), indicating that the dominance is in the direction of earlier heading time; while from the sign of δ of plant height (which is positive) we also see that the progeny mean is greater than

Table 2. *Estimates of the second degree statistics, mean values and heterosis, obtained from a diallel cross for the O. sativa experiment*

Statistics	Heading time	Plant height
V_p	16.2080	389.3800
$\bar{V}_r$	7.4440	120.6512
$V_{\bar{r}}$	1.6933	89.3005
$\bar{W}_r$	3.9912	180.2800
$\bar{P}$	87.9600	110.0000
$\bar{F}_1$	84.0400	119.0200
$\frac{1}{2}\delta = (\bar{F}_1 - \bar{P})$	-3.9200	$+9.0200$
Heterosis	-4.5%	$+8.2\%$

the parental mean, indicating that the dominance is in the direction of greater plant height.

The results of the homogeneous test of $(W_r - V_r)$ shows that the corresponding diallel cross conforms to the Hayman's Hypothesis (1954b) for both characters. However, it is posible to draw the (V_r, W_r) graph (Fig. 1 and 2), and to make estimation of the various genetical components, such as D, F, H_1, H_2, δ^2, E, and $(D-H_1)$. The results are given in Table 3.

Table 3. *The value of genetical components and their standard error for heading time and plant height*

Genetical component	Heading time	Plant height
D	15.1200 ± 2.1615	376.2568 ± 8.9295
F	15.1456 ± 5.3995	41.8922 ± 19.7797
H_1	27.1904 ± 5.8375	116.7445 ± 24.1151
H_2	20.8268 ± 5.2946	99.1564 ± 21.8726
δ^2	60.1600 ± 3.5746	317.0428 ± 14.7672
E	1.0880 ± 0.8824	13.1232 ± 33.6454
$(D-H_1)$	-12.0704 ± 5.1877	259.5123 ± 21.4307

3. Distribution of alleles

The mean value of the product of gene frequencies of dominance and recessive alleles at the loci of dominance may presented by $\overline{uv} = H_2/4H_1$. If $\overline{uv} = \frac{1}{4}$, then $\bar{u} = \bar{v} = \frac{1}{2}$, i.e., the positive and negative allelss at these loci are in equal proportions in the parents. A summary of the results of the genetic analysis when applied to heading time and plant height is given in Table 4. Here, the estimated value of $\overline{uv}$ is 0.20 and 0.21 for heading time and for plant height, respectively, that is to say, $\bar{u} \neq \bar{v} \neq \frac{1}{2}$ for both characters. This results

is in agreement with the result obtained from the analysis of variance (Table 1), in which H_1 was shown to be not significantly different from H_2, $[(b_2)^*]$. From Table 3, we see that $H_1 > H_2$ for both characters, *i. e.*, the positive and negative alleles at these loci are not in equal proportions in the parental varieties.

Table 4. *Genetic analysis of heading time and plant height*

Statistics	Heading time	Plant height
$\overline{uv}$	0.20	0.21
K_d/K_r	2.20	1.20
n	3.00	3.20
h^2	0.1542 ± 0.3077 (not sig.)	0.8766 ± 0.1871 (sig., $P < 0.01$)

4. Regression analysis

The information from the regression analysis is remarkably not in conformity over the two characters. Analysis of the data for heading time (Fig. 1) gave a significant regression value $b = 0.6437 \pm 0.0518$ ($P = 0.05 \sim 0.01$); but this slope is significantly different from the unit slope ($P < 0.01$). This can be interpreted as indicating the presence of non-allelic interaction, particularly complementary gene action, between parental gene combinations. In the analysis of the data of plant height (Fig. 2), we obtained a regression line
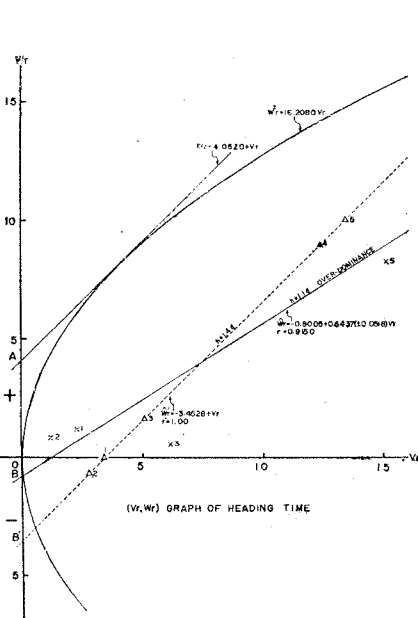

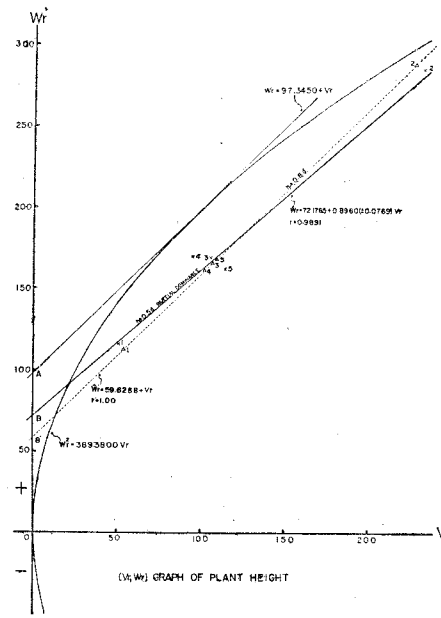Fig. 1.   (V_r, W_r) graph of heading time.

Fig. 2.   (V_r, W_r) graph of plant height.

with a slope $b = 0.8960 \pm 0.0769$ (P<0.01). This is not significantly different from the unit slope, indicating that only additive and partially dominant genes existed between the parental gene combinations and that genic interaction did not exist.

5. *The degree of dominance*

We used three methods to estimate the degree of dominance, *i. e.*, $(H_1/D)^{1/2}$, $(AB/AO)^{1/2}$, and $(AB'/AO)^{1/2}$, where the values of $(AB/AO)^{1/2}$ and $(AB'/AO)^{1/2}$ were estimated from the regression analysis (Fig. 1 and 2), while the latter was estimated after the environmental variation had been eliminated.

In the character of heading time, Fig. 1 shows that the regression line cuts the ordinate below the origin (as B and B'), indicating the presence of over-dominance in some of the crosses, while in the character of plant height (Fig. 2), the regression line cuts the ordinate above the origin (as B and B'), indicating the presence of partial-dominance in some of the crosses. We observe that these three estimation methods have the same results as shown in Table 5.

Table 5. *Estimates of the degree of dominance*

Formula	Heading time	Plant height
$(H_1/D)^{1/2}$	1.3	0.6
$(AB/AO)^{1/2}$	1.1	0.5
$(AB'/AO)^{1/2}$	1.4	0.6
Degree of dominance	Over-dominance	Partial-dominance

The ratio (K_d/K_r) of the total numbers of dominant to recessive genes in all the parents is 1.2 for plant height (Table 4), which is close to unity, implying proximity between the numbers of dominant and recessive alleles in the parent. But in the character of heading time, the value of this ratio is nearly 2.2, indicating that the total numbers of dominant genes is two about times greater than that of recessive ones.

6. *Number of genes*

The ratio δ^2/H_2 may be used to estimate the number of gene groups which control the character and exhibit dominance to some degree. From Table 4 we see that the value of n ($= \delta^2/H_2$) is nearly 3.0 for both characters. So it may be inferred that there were at least three gene groups controlling heading time or plant height having some degree of dominance.

7. *Dominance and size*

In the character of heading time, the order of dominance of the parents determined by $(W_r + V_r)$ is 21345, and the order of heading time $(\bar{X})$ is 23514;

the correlation between $\bar{X}$ and $(W_r + V_r)$ is 0.6 (not sig.), corroborating our results of Section 2, that heading time is dominant, with Wu-no-tao (parent 2) being the earlist in heading time and carrying most of the dominant genes.

In the character of plant height, the order of dominance of the parents obtained from $(W_r + V_r)$ is 34251, and the order of plant height $(\bar{X})$ is 14352; the correlation between $\bar{X}$ and $(W_r + V_r)$ is —0.35 (not sig.). This result is in good agreement with the result of Section 2, i.e., plant height shows partial-dominance with the variety Yen-no (parent 1) being the highest and carrying most of the dominant genes.

8. *Heritability*

The heritability (h^2) was estimated by the method of regression of the mean values of F_1 offspring on the value of mid-parent. The results is also given in Table 4. From this results, we know that the heritability of plant height is very high, close to 88% (P<0.01, Fig. 3); but the heritability of heading time is rather low, only nearly 15%. (not sig., Fig. 4)
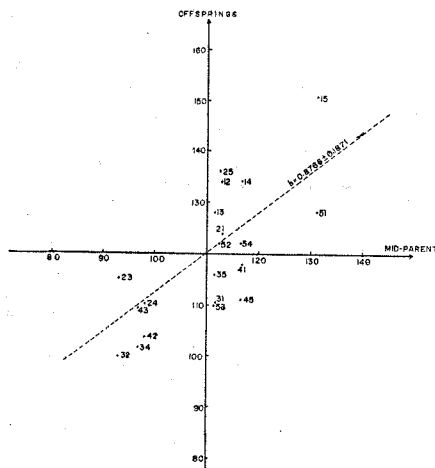

Fig. 3. Relationship between the mean value of offspring and mid-parent, and the heritability of plant height.
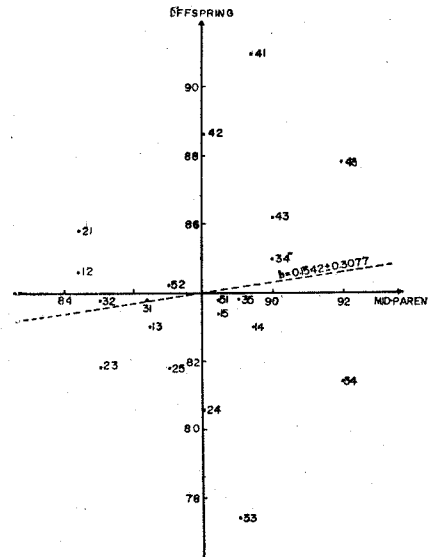
Fig. 4. Relationship between the mean value of offspring and mid-parent, and the heritability of heading time.

From the above results, we may conclude that:

1. The genetic mechanism of plant height is relatively simple as compared with that of heading time.

2. The plant height is rather stable in its response to environmental variation; but the heading time is much less stable.

3. There are two methods for increasing the rate of response to selection: one by increasing the heritability and the other by reducing the proportion selected thereby increasing the intensity of selection (Falconer 1960). In view of our results obtained above, we must increase the selection intensity in plant height and increase the heritability for heading time so as to increase the rate of selection response in the early generations; but the heritability of heading time can be increased only by reducing the environmental variation through careful rearing and management.

Summary

In this paper, a study of basic nature on the quantitative inheritance of rice were carried out by means of 5×5 diallel crosses with a view to estimating the genetical components and their standard errors from the second degree statistics according to Hayman's methods (1954a, b), and to estimating genetic parameters such as additivity, dominance, heterosis, distribution of alleles, number of gene groups, dominance and size of each variety, and the heritability for heading time and for plant height in F_1 progeny.

水 稻 數 量 性 狀 之 遺 傳 研 究

I. 雜種第一代抽穗期及株高之全互交分析

鄔 宏 潘

本研究係利用五水稻品種進行全互交，以研究水稻數量性狀之遺傳現象。本報告為利用 F_1 及親本之自交後代為資料，依據 Hayman 氏 (1954a, b) 之統計分析原理及方法研究水稻之抽穗期及株高等數量性狀之遺傳。其主要結果有：

1. 在此二性狀中，由品種間平均效果所引起之遺傳變異甚大，同時此二性狀皆具有單向之顯性因子作用。以抽穗期早者或株高高者為顯性。

2. 抽穗期遺傳受細胞質之影響，而株高則可能微受影響。

3. 支配抽穗期或株高之顯，隱性之因子頻度不相等。

4. 從廻歸分析之結果知，抽穗期為超顯性，具有非相對因子間之交感作用，而株高為部份顯性，缺少非相對因子間之交感作用。

5. 抽穗期較株高易受栽培環境之影響。

6. 支配抽穗期之顯，隱性因子總數，略為相等，但顯性因子數略多，而支配株高者，則顯性因子總數大於隱性因子總數 2 倍之多。

7. 至少有 3 羣因子各別支配抽穗期或株高之遺傳。

8. 供試 5 品種中，在抽穗期方面，以烏糯稻之顯性因子數最多，其抽穗期亦較早。在株高方面，則以岩糯之顯性因子數最多，其株高亦最高。

9. 抽穗期及株高之雜種優勢皆不太大。

10. 抽穗期之遺傳率甚小（15%）而株高則甚大（88%）。

從以上之結果知，株高之遺傳構成顯然較抽穗期簡單，而對環境之反應亦較穩定，因此在雜交後代早期選種時其效果較抽穗期為大。如欲提高抽穗期之選種效果，則需力求環境變異之減少。

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