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Study of Quantitative Inheritance in Some Mutants of Rice

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STUDY OF QUANTITATIVE INHERITANCE IN SOME MUTANTS OF RICE

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Ph.D. Thesis

By

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June, 1994

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Dedicated

to

my

Parents

DECLARATION

I, hereby, declare that the entire work now submitted as a thesis towards the fulfilment for the degree of Doctor of Philosophy at the University of Rajshahi, Rajshahi, Bangladesh, is the result of my own investigation.

I, further, declare that the work emboided in this thesis has not been submitted previously or concurrently as a candidature for any other degree.

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The Author

STUDY OF QUANTITATIVE INHERITANCE IN SOME MUTANTS OF RICE

ABSTRACT

Nine agronomic characters viz., plant height, effective tillers per plant, panicle length, flag leaf length, flag leaf breadth, flag leaf area, primary branches per panicle, grains per panicle and grain yield per plant of rice (*Oryza sativa* L.) were studied in two separate investigations. Biometrical techniques were applied in analyzing the data.

Gene Action : Inheritance of nine agronomical characters were studied in a single cross of rice (*Oryza sativa* L.) using segregating (F_2, F_3, B_1 and B_2) and non-segregating (parents and F_1) generations. The means of segregating and non-segregating generations (F_1, F_2, F_3, B_1 and B_2) were within the parental ranges in all the characters. Both additive and non-additive types of gene effects were involved in the inheritance of these characters but the former was of much importance than the latter. Epistatic gene effects were detected. The absolute magnitude of epistatic gene effects was always less than the mean effect. Additive x additive (i) type of epistasis was more pronounced in most of the characters. Duplicate type of epistatic gene effects was observed in most of the cases. Additive (D) type of genetic variation formed the major part whereas dominance (H) type of

genetic variation contributed very little to the phenotypic variation in all the cases. All type of heritability estimates were high in most of the cases. Broad sense heritability (Hb) ranged from 41.27% for panicle length to 80.24% for grain yield per plant. Narrow sense heritability (Hn) ranged from 98.18% for panicle length to 143.19% for plant height. Heritability estimated by parent offspring regression ranged from 68.42% to 108.33% for panicle length and plant height, respectively. Partial dominance in F_1 and F_2 and both partial and overdominance in F_3 were noticed. No linkage was detected for all the characters. Positive isodirectionally distributed polygenes for all the characters were common in the parents. Number of effective factors were 2-3 in majority of the cases.

Genotype - environment interaction : G X E interactions were investigated for nine agronomic characters of rice (*Oryza sativa* L.) with the same parents and generations (used in the Part I study) under eight artificially created soil environments of N, P and K fertilizers. Genotype-environment interactions were operative in both the segregating and non-segregating generations. Both the linear and non-linear functions were accounted and greater portion of G X E interactions were accounted by the linear functions of the environmental means. These two components of G X E interaction were under the control of different gene system. A real difference between the genotypes existed in relation to response and stability. Genetic diversity

in the generations was indicated. Significant effects of different environments were detected in all the cases. The generations had varied responses to the environmental changes. Association of mean with response for all the characters was observed. On the other hand association of stability with mean and response was absent. When association of these three aspects ($\bar{X}$, b_i and $\bar{S}^2_d$) were examined between characters, means and responses were found to be well associated while stability was not associated in most of the characters. Same gene system control for mean and response and different gene system control for stability were noticed. Nature of inheritance of mean was detected. Additivity played the major part in the inheritance of these characters. Duplicate types of gene actions were noticed in two of the studied characters. All the fertilizers (N, P and K), when applied singly, had favourable effects but N had the greatest effect than the other two fertilizers. On the basis of mean, response and stability, selection can be made for all environments from F_2 and F_3 generations.

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INTRODUCTION

Rice is the principal food crop of tropical and subtropical regions and second most important food crop of the world. In China, India, Japan, Southeast Asia and in the adjacent islands of the Pacific over 85 percent of the world's rices are grown. China and India produce about 50% of the total world's production while Japan, Indonesia, Pakistan, Burma, Thailand, Indochina and Bangladesh produce about 30 percent of world's rice production.

Rice is one of the oldest cultivated crops and has been cultivated in China and India for at least 5000 years. It is believed that rice has originated in Southeast Asia since large areas of marshy land suitable for its cultivation exist in this area. From there rice has likely spread eastward into China.

Most of the countries of Asia and Africa are deficit in food production and they are suitable for rice cultivation. Hence, rice plays an important role in the economy of these countries.

Usually poor countries are facing the problem of food crisis and they are trying to increase the production of food crops. This is being done not only by acclimatization of introduced better exotic varieties as food crops to new areas but also by evolving high yielding varieties through hybridization and selection. The latter has a greater probability in achieving the goal. Thus plant breeders and agronomists have a great role to play in solving the problems. Of the breeding procedures

crossing, selection and inheritance study of characters are the important aspects. Thus, plant breeders' principal objectives in breeding rice are yield; maturity; resistance to lodging, disease and insect; quality and varietal adaptation for specific environments such as drought and saline areas.

The present investigation comprises two parts. The first part deals with the yield and some yield components and with some leaf characteristic of a cross between two rice mutant lines. The second part includes the genotype-environment interaction of different generations of the above said cross with eight artificially created soil conditions.

PART - I

GENE ACTION

REVIEW OF LITERATURE

In the segregating progenies quantitative characters show a continuous variation which forms the basis of evolution and has served the practical purposes of plant and animal improvement. Rediscovery of Mendel's laws of heredity could not create much interest of the breeders to handle continuous variation as means of plant and animal improvement in earlier breeding work because the mathematical techniques required to interpret the results of continuous variation, were lacking.

Until the genetical assumptions and biometrical methods developed in the early part of this century, the fundamental nature of gene action and interactions involve in the inheritance of quantitative characters were not well understood. In 1909, for the first time, Johannsen published the theory of pure line selection in which he clearly distinguished heritable and non-heritable variances. This made the investigators to become interested in studying continuous variation as genetical aspect. In the same year (1909) Nelsson-Ehle stated his multiple factor hypothesis. East (1915) studying the inheritance of quantitative characters of *Nicotiana rustica* L. clearly showed that quantitative characters were inherited with the joint action of genetical and environmental factors. He also showed that the quantitative characters were inherited according to Mendel's laws of inheritance.

In 1918, Fisher studied the genetic variance in relation to environmental effect. He was the first to provide statistical methods of partitioning the total variation into genetical and environmental components. He suggested that several genes acted simultaneously on a quantitative character producing the total variation. He developed techniques for detecting the average main (additive) and dominance effects of the genes even when the genes were unequal in effect and exhibited incomplete dominance.

Later on, two lines of statistical techniques were developed to measure the gene action and interaction involved in continuous variation. According to the first, the first degree statistics (mean) of different generations were used to separate components of variation. Mather (1949) developed biometrical techniques based on mathematical models of Fisher *et al.* (1932). He described how the main(additive) and dominance variation could be estimated in wide variety of genetical experiments.The other statistical technique used the second degree statistics (variance and covariance) of different generations for the analysis of continuous variation present in random mating groups (Mather, 1949). It involved in partitioning the total variation of a population into heritable and non-heritable components. Heritable component was further partitioned into fixable heritable i.e. variation due to additive gene effect (D) and non-fixable heritable i.e. variation due to dominant gene effect (H). In partitioning the heritable components into D and H it requires

minimum three segregating generations (B_1, B_2 and F_2) and non-segregating generations (P_1, P_2 and F_1) related to segregating generations. Estimates of D and H from three segregating generations do not allow sufficient statistics to test the significance of these components (Mather, 1949). Later on Mather (1949) developed least square technique to estimate heritable and non-heritable components from the cross between two inbred lines and their selfed generations (F_2 and F_3). Inclusion of F_3 generation provided sufficient statistics in the estimation of heritable and non-heritable components which allowed the estimation of standard error (S.E.) of different components. Hill (1966) have included backcross generation and different types of generations developed from crossing to different parents and selfing and backcrossing the first backcross generations for the estimation of different types of heritable and non-heritable components. The work of Fisher *et al.* (1932) influenced several investigators such as Yates (1947), Comstock and Robinson (1948), Mather (1949), Anderson (1953), Anderson and Kempthorne (1954), Kempthorne (1954), Jinks (1954), Hayman (1954), Hayman (1957), Hill (1966) and others to work on the gene action and interactions in continuous variations and thus, most of the genetic models to study continuous variation came into existence. Anderson and Kempthorne (1954) provided all the information about additive, dominance and digenic epistatic variation through six-parameter model. Hayman (1958)

successfully separated additive and dominance effects from epistasis by using three-parameter and six-parameter models. He suggested that means of families or generations were influenced by epistasis which often became as great as additive or dominance variation and it might be present in the form of interaction with additive effect, with dominant effect or with both additive and dominant effects. However, additive and dominant gene effects cannot be uniquely measured when significant epistasis is present and the relative contribution of the types gene action to various genetic phenomena such as heterosis cannot be ascertained by the partitioning method of Hayman (1960). On the other hand, estimates of the parameter do produce an indication of the relative importance of the various types of gene effects effecting the total genetic variation of an attribute. Later Mather and Jinks (1971), however, interpreted heterosis on the basis gene effects as described by Hayman (1958). Many investigators have worked on the inheritance of quantitative characters and on the nature of gene action involved in the inheritance of quantitative characters in rice, some of which are discussed below. Chang *et al.* (1965) in 1-geo-tze Taiwan and Aquino and Jennings (1966) and Heu *et al.* (1968) in Taichung Native-1 found that one recessive gene, which was positively related to yield, controlled the short stature. Intercrosses among 1-geo-tze, Dee-geo-woo-gen and Taichung Native-1 showed that the recessive gene in all three semi-dwarf belongs to the

same locus (IRRI, 1967, p. 67-68). Chang and Vergera (1972) reported that a second recessive gene, non-allelic to the recessive gene of Taiwan's semi-dwarf, was found to control short plant stature in B 5580 AI-15. In the study of diallel crosses, earlier heading time was found to be regulated by predominantly dominant genes or by dominant genes with little non-allelic interaction while plant height was found to be controlled mostly by genes with additive effect and also by some genes showing dominance (Wu, 1968; Li and Chang, 1970 and Khaleque and Eunus, 1975). Mohammed and Hanna (1965) showed that plant height, in cross Sabini x Pakistan-7, was controlled by two pairs of effective factors with partial dominance. Polygenic control of length of panicle was also reported by them in 1965 and they noted that longer panicle length was dominant over shorter one. Polygenic control of plant height and of many other characters was also observed by Mitra (1962), Rajagopalon *et al.* (1973) and Khaleque (1975). Sathyanarayaniah and Reddi (1973), in a cross between IR8 and WC1263, found that earlier heading time and plant height was controlled by dominant gene while Rajendran and Namboodiri (1971), in Indica x Japonica and Indica x Indica crosses, noted multiple genic inheritance of these two characters.

Evaluation of genetic structure of panicle number, panicle length and spikelet number revealed that the gene action regulating these characters was largely additive, though some

loci showing dominance, was also noted (Li and Chang, 1970). Additive type of gene action regulating tiller number, panicle number and panicle length was also detected by Wu (1968).

Regarding grain weight Chandraratna and Sakai (1960) estimated 10 additive genes for this character in a cross between two Ceylonese varieties. Wu (1968) in F_1 generations and Li and Chang (1970) in F_1 and F_2 generations observed that the high count of tillers or panicles, longer panicles and larger number of spikelets were partially dominant to low count of tillers or panicles, shorter panicles and fewer number of spikelets respectively. Rahman and Eunus (1973) noted in F_1 generations that additive and dominant genetic variations were greater for panicle length and primary branch number than those for spikelet number and grain yield per panicle.

Kaul (1972) when studying the growth performance of Basumati-370, Jhona-349, IR 8, Jaya and Padma found that plant height was highly heritable character followed by grain weight, tiller number per plant, panicle length and grain number per panicle. Kaul and Bhan (1974) also found high heritability for grain number per panicle, effective tiller number per plant and culm length in 30 varieties. They also showed high expected selective limit for these characters. High broad sense heritability was observed in rice by Khaleque (1975).

Ali *et al.* (1975) studied F_1, F_2 and F_3 generations of the crosses Giza-159 x IR 8 and Giza x Taichung Native-1. They

observed that the estimates of dominance genetic variance were significantly positive and of additive genetic variance were significantly negative. Shaalan *et al.* (1975) studied grain yield per plant, number of ear bearing tillers per plant and panicle length in two crosses and found almost similar results.

Estimates of high heritability and genetic advance were obtained by Maurya (1976) for 13 traits in 21 F_1s and F_2s derived from seven parents revealed that improvement in grain yield could best be effected by selection for high grain number per panicle and long grains.

Chaudhury *et al.* (1976) observed in crosses AC-1951 x TN-1 and Tainan-3 x AC-1951 that broad sense heritability and estimates of genetic advance were high or moderately high for plant height, number of ear bearing tillers, panicle length, number of spikelets per panicle, 100 grain weight and single plant yield. They also showed that at least one pair of genes were controlling each of these characters.

Singh and Nanda (1976) studied a 6 x 6 diallel cross. They found overdominance for yield per plant and panicle length and partial dominance for panicle number per plant. They showed that additive and dominant genes were important for yield per plant while additive genes were of major importance for panicle length and panicle number per plant. Recessive genes were more important in respect to panicles per plant whereas dominant genes were more important for yield per plant and panicle length.

Shaalai and Aly (1977) while studying the progenies of the crosses Nahda x IR 8 and Nahda x Taichung Native-1 found significant additive genetic variance for plant height and number of tillers per plant in both crosses. They also found significant dominance genetic variance for number of tillers and number of ear bearing tillers in the first cross and for plant height, number of tillers, number of ear bearing tillers and panicle length in the second cross. They observed high broad sense heritability in most of the characters of the two crosses. They also found high genetic advance for panicle length of cross 1 and for number of tillers and number of ear bearing tillers of cross 2. Khaleque and Eunus (1977) also reported high broad sense heritability for seeding to heading period, size of flag leaf, length of panicle, number of primary branches per panicle, number of kernel per panicle, 100 kernel weight and yield per plant of 1 to 2 boro growing rice varieties. They also noted high expected selective limit for the size of flag leaf, number of primary branches per panicle, number of kernel per panicle and yield per plant. Prasad and Chandra (1977) estimated moderately high broad sense heritability for plant height, area of second leaf, total grain number per panicle and grain weight per panicle. They showed the highest estimate of selective limit for grain yield per plant.

Kim and Heu (1977) while evaluating a diallel cross and it's F_2 generations suggested that the additive effects were the main

source of variation in highly heritable culm length. Significant additive effect for culm length and plant height for 14 varieties was detected by Yen (1977). He detected significant dominant effect for plant height and suggested that at least one pair of gene was involved in controlling each of these characters.

Azam (1981) studied F_2, F_3 and parental populations of two single crosses involving four varieties of rice. He observed additive genetic variances of yield and yield components were of more importance while dominance variations of these characters were mostly non-significant. Heritability was generally low and linkage was detected. Number of effective factors in most of the characters were detected by him to be one. He also found the presence of overdominance in most of the cases. He observed that either plus or minus genes appeared to be isodirectionally distributed in some characters while in other characters plus or minus genes were nonisodirectionally distributed.

Using a 6 x 6 diallel cross of cultivars and dwarf mutants, Kumar *et al.* (1986) estimated additive-dominance gene action in plant height. He found that the plant height was governed predominantly by additive genes with dominance gene action and it possessed high heritability.

Hahn and Chae (1987) estimated some genetic parameters of grain yield and some grain characters in four semidwarf rice varieties crossed in all possible combinations to give single, double, 3-way and backcross hybrids. He studied the additive and

dominance gene action in single crosses and found that the additive effects were of much importance followed by heterosis effects for most of the characters. He found the presence of epistasis and estimated significant heterosis for all characters except grain width. Average heterosis that he assessed, was negative for certain traits and positive for the others. He also observed that heterosis was more important for yield.

F_1, F_2 and backcross generations were studied by Tai *et al.* (1989) in crosses of *O. nivara* Japonica cultivars. They observed broad sense heritability were high for various traits while narrow sense heritability values were greatest for stem length, panicle length, spikelets/panicle and percentage of grain set.

Yan and Wang (1990) studied F_1 and F_2 generations of 11 indica-japonica hybrids. They found high broad sense heritability in length, breadth, area and angles between main stem and leaves. They found that the first 3 traits (length, breadth and area of leaves) were governed by at least two pair of genes. They also found significant positive estimates of heterosis in these 3 leaf characters and negative for the other 3 traits.

Ten characters were assessed by Choi (1990) in F_1, F_2 and BC_1 generations of the semidwarf indica cultivar IR29 crossed with the early maturing japonica variety Cheolweon 1. He observed heterosis for culm and panicle length, spikelets/panicle and early maturity in the F_1 plants. He also observed that dominant epistasis influenced heading time while complementary or multiple

type non-allelic interactions were involved in culm length.

Information on the nature of gene actions and their interactions influencing different economic characters of rice is not adequate, specially with respect to yield and yield components. The purpose of the present investigation was, therefore, to study the inheritance of nine quantitative characters of rice (*Oryza sativa* L.) using mainly the means and variances and covariances of different generations.

MATERIALS AND METHODS

A. MATERIALS

The materials used in this experiment consisted of two stable rice mutant lines (obtained from a local rice variety, Nizersail, irradiated in 1973) and F_1, F_2, F_3, B_1 and B_2 generations of single cross made between these two rice mutant lines. Some salient features of these two mutant lines used as parents are described below in brief:

Mut NS1 : Tall, moderate early maturing, possesses more number of tillers, leaves are long-board, panicles are longer which bear a good number of grains and high yielder type. This mutant line was released in 1987 by Bangladesh Institute of Nuclear Agriculture under the commercial name "Binasail".

Mut NS3 : Semi - dwarf, early maturing, possesses lower number of tillers, leaves are small and moderate broad, panicles are smaller which bear less number of grains and low yielder type.

B. METHODS

The methods used in this study is described under the following sub-heads :

a) Production of Experimental Seeds,

b) Preparation and Design of Experimental Field,

c) Setting of Experiment in the Field,

d) Collection of Data, and

e) Techniques of Analysis.

a) Production of Experimental Seeds

Seeds of two mutant lines viz., Mut NS1 and Mut NS3 were obtained from the Plant Breeding Division, Bangladesh Institute of Nuclear Agriculture, Mymensingh, Bangladesh. These two mutant lines were raised and grown in pots during the T. aman season of 1988 and sufficient number of F_1 seeds (about 300) were produced by crossing Mut NS3 as P_1 with Mut NS1 as P_2 (Mut NS3 x Mut NS1). In the subsequent year F_1 plants were grown in field during the T. aman season. Some of the F_1 plants were used to produce backcross seeds. The backcross seeds were produced by crossing F_1 plants with the parents ($B_1 = P_1 \times F_1$ and $B_2 = P_2 \times F_1$). From remaining F_1 plants F_2 seeds were harvested separately. For producing F_3 seeds, 50% of the harvested F_2 seeds were sown and F_2 plants were raised in the T. aman season of 1990. These F_2 plants were harvested separately and F_3 progeny seeds were collected. The remaining 50% F_2 seeds were kept for setting final experiments. Following the same cross combination fresh F_1 seeds were produced in the same year. Thus, the seeds of F_1s, F_2s, F_3s, B_1s and B_2s were produced for setting experiments.

For crossing healthy and disease-free plants were selected. Emasculation was then done in the early morning by removing anthers from flowers before they open. The emasculated plant was

treated as female plant. On the eve of emasculation, all the required instruments including hands were sterilized with rectified spirit soaked cotton. During emasculation the upper portion of the panicles as well as the flowers from the lower portions of the panicles were cut off by a sterilized scissor. Thus 20-25 spikelets were kept in the middle portion of the panicles. Then all the anthers were carefully removed with the help of a fine pointed forcep. After emasculation the operated flowers were further examined under a hand lens to became sure that no anthers or parts of anthers were left in the emasculated flowers. The emasculated panicles were then labelled and covered with fine porous polythene bags to prevent contamination by foreign pollens and to facilitate transpiration. On the next morning of emasculation, when the matured spikelets of the selected male parent just opened, anthers were collected. Then the pollination was done by rubbing the bursted anthers on the stigma of the emasculated flowers. The pollinated panicles were then covered with porous polythene bags and labelled properly. After two days of pollination, these panicles were uncovered by removing the polythene bags, crossed plants were examined and these were allowed to develop. The fully matured grains were collected along with the labels, dried well and stored in a desiccator.

b) Preparation and Design of Experimental Field

The experiment was carried on at the Farm of Bangladesh

Institute of Nuclear Agriculture, Mymensingh. The soil of the field was clay loam. By repeated ploughing, cross-ploughing and harrowing the field was made homogenous. Before final, preparation of the land triple super phosphate (TSP) muriate of potash (MP), zinc sulphate (Zn) and gypsum (sulphur) fertilizers were applied at the rate of 136, 66, 14 and 56 kg/ha, respectively. Urea (128 kg/ha) was applied in 3 splits. The first split was applied after 7 days of transplanting and the second and third splits were applied at the time of maximum tillering and panicle initiation stages for maximum utilization of urea fertilizer.

The whole experimental field comprised an area of 7.2m x 10.5m in size. The experimental field was then divided into three blocks of 3.0 m x 7.2m size for replicating the experiment. The space between the plants, between the rows and between the replications (blocks) were 15 cm, 20 cm and 75 cm, respectively. There were 1.0 m footpaths all around the experimental field.

c) Setting of Experiment in the Field

The experiment was set in the field of Bangladesh Institute of Nuclear Agriculture, Mymensingh, in the first week of August, 1991, with the seedlings of all the non-segregating (P_1, P_2 and F_1) and segregating (F_2, F_3, B_1 and B_2) generations. Before that seedlings of all these generations were raised in the seed beds. Seeding was done on 4th July, 1992. For setting the experiment 30 days old seedlings were used and transplantation was done on

3rd August, 1991, in the sequence as follows : P_1 in 2 rows, F_1 in 1 row, 15 F_2 families in 15 rows, 15 F_3 families in 15 rows, B_1 in 1 row, B_2 and 1 row and P_2 in 2 rows in each plot (3.0m x 7.2m). The experiment was replicated thrice. The two parents were kept at the two ends of the plots so that the outer rows of the two parents served as the guard lines. Thus, there were altogether 35 experimental rows in a plot. Each row was 3.0 m long and consisted of 21 plants with 15 cm spacings between the plants. The space between the rows and between the plots were 20 cm and 75 cm, respectively.

Irrigation and other usual cultural practices were done whenever necessary.

d) Collection of Data

Data on some agronomical characters, leaf characters and grain yield were recorded on individual plant basis from 10 randomly selected plants (excluding the border plants) per line. Total number of plants from which data were collected from different generations are shown below :

Generations	Number of rows per generation	Total number of plants taken for data
P_1	1	10 x 1 x 3 = 30
P_2	1	10 x 1 x 3 = 30
F_1	1	10 X 1 X 3 = 30
F_2	15	10 x 15 x 3 = 450
F_3	15	10 x 15 x 3 = 450
B_1	1	10 x 1 x 3 = 30
B_2	1	10 x 1 x 3 = 30

The following characters were recorded from the selected plants :

1. Plant height (PH) : It was measured in cm from the base to the tip of the longest tiller.

2. Effective tillers/ plant (ET/P) : Number of effective tillers in a plant was counted.

3. Panicle length(PL) : It was measured in cm from the base to the tip of the panicle of the longest tiller.

4. Flag leaf length (FLL) : It was measured in cm from the base to the tip of the flag leaf of the longest tiller.

5. Flag leaf breadth (FLB) : It was measured in cm from the broadest part of the flag leaf of the longest tiller.

6. Flag area (FLA) : It was obtained by multiplying the length of the flag leaf with breadth and a constant (0.67) and was expressed in cm^2. The constant was used because of shape of the leaf.

7. Primary branches per panicle(PB/P) : Number of primary branches in the longest panicle which was taken for measuring panicle length.

8. Grains per panicle: (G/P) Number of filled grains in the longest panicle which was taken for measuring panicle length.

9. Grain yield/plant: (Gy/p) It was the weight of total filled grains in gm taken by threshing all the grains of a plant.

e) Techniques of Analysis

The biometrical techniques of analysis developed by Mather (1949) based on the mathematical models of Fisher *et al.* (1932)

and those of Hayman (1958) and Allard (1960) were followed for analysing the collected data.

Means and Standard Errors (S.E.)

The data from the three replications were pooled to compute means, variances and standard errors of each population by the following formulae :

Mean ($\bar{X}$) $= \Sigma X/n$

Variance (σ^2) $= [\Sigma X^2 - (\Sigma X)^2/n]/(n-1)$

Standard error (S.E.) $= (\sigma^2/N)^{1/2}$

Where, X is the individual observation, n is the total number of observations and Σ = Summation.

Theoretical Means

The theoretical arithmetic and theoretical geometric means were computed for F_1, F_2, F_3, B_1 and B_2 generations following the technique of Burton (1951) :

i) Theoretical Arithmetic Means:

$$\bar{F}_1 = 0.50\ (\bar{P}_1 + \bar{P}_2)$$

$$\bar{F}_2 = 0.25\ (\bar{P}_1 + \bar{P}_2 + 2\bar{F}_1)$$

$$\bar{F}_3 = 0.25\ (\bar{P}_1 + \bar{P}_2 + 2\bar{F}_2)$$

$$\bar{B}_1 = 0.50\ (\bar{P}_1 + \bar{F}_1)$$

$$\bar{B}_2 = 0.50\ (\bar{P}_2 + \bar{F}_1)$$

ii) Theoretical Geometric Means:

$$\bar{F}_1 = \text{Antilog}\ [0.50\ (\log\bar{P}_1 + \log\bar{P}_2)]$$

$$\bar{F}_2 = \text{Antilog}\ [0.25\ (\log\bar{P}_1 + \log\bar{P}_2 + 2\log\bar{F}_1)]$$

$$\bar{F}_3 = \text{Antilog}\ [0.25\ (\log\bar{P}_1 + \log\bar{P}_2 + 2\log\bar{F}_2)]$$

$$\bar{B}_1 = \text{Antilog } [0.50\ (\log\bar{P}_1 + \log\bar{F}_1)]$$

$$\bar{B}_2 = \text{Antilog } [0.50\ (\log\bar{P}_2 + \log\bar{F}_1)]$$

Scaling Test

Mather (1949) and Mather and Jinks (1971) showed that owing to the presence of epistatic gene action the means of B_1, B_2, F_2 and F_3 generations would deviate from their expectations. For each generation, they developed scaling test separately which they designated as A, B, C and D related to B_1, B_2, F_2 and F_3 generations respectively. These are as follows -

$$A = 2\bar{B}_1 - \bar{P}_1 - \bar{F}_1$$

$$B = 2\bar{B}_2 - \bar{P}_2 - \bar{F}_1$$

$$C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2 \quad \text{and}$$

$$D = 4\bar{F}_3 - 2\bar{F}_2 - \bar{P}_1 - \bar{P}_2$$

Variances of A, B, C and D were calculated as follow -

$$V_A = 4V\bar{B}_1 + V\bar{P}_1 + V\bar{F}_1$$

$$V_B = 4V\bar{B}_2 + V\bar{P}_2 + V\bar{F}_1$$

$$V_C = 16V\bar{F}_2 + 4V\bar{F}_1 + V\bar{P}_1 + V\bar{P}_2 \quad \text{and}$$

$$V_D = 16V\bar{F}_3 + 4V\bar{F}_2 + V\bar{P}_1 + V\bar{P}_2$$

Where,

$$V\bar{P}_1 = (S.E.\bar{P}_1)^2/r$$

$$V\bar{P}_2 = (S.E.\bar{P}_2)^2/r$$

$$V\bar{B}_1 = (S.E.\bar{B}_1)^2/r$$

$$V\bar{B}_2 = (S.E.\bar{B}_2)^2/r$$

$$V\bar{F}_1 = (S.E.\bar{F}_1)^2/r$$

$$V\bar{F}_2 = (S.E.\bar{F}_2)^2/r \quad \text{and}$$

$$V\bar{F}_3 = (S.E.\bar{F}_3)^2/r$$

Where, r is the number of replication.

Standard error of A, B, C and D were determined in the following way -

$$S.E._A = (V_A)^{1/2}$$

$$S.E._B = (V_B)^{1/2}$$

$$S.E._C = (V_C)^{1/2} \quad \text{and}$$

$$S.E._D = (V_D)^{1/2}$$

In these estimation, if A=0, B=0, C=0 and D=0 then it will indicate that either epistasis is absent or epistasis do effect the mean of B_1, B_2, F_2 and F_3 generations, respectively. But where, A≠0, B≠0, C≠0 and D≠0 then it will indicate that epistasis is present in B_1, B_2, F_2 and F_3 generations respectively.

Epistatic Gene Effect

i) 3-Parameter Model:

The expectation of generation means in terms of segregating and non-segregating generations were as follows -

$$\bar{P}_1 = m + d$$

$$\bar{P}_2 = m - d$$

$$\bar{F}_1 = m + h$$

$$\bar{F}_2 = m + 1/2h$$

$$\bar{F}_3 = m + 1/4h \qquad \text{(Equation 1)}$$

$$\bar{B}_1 = m + 1/2d + 1/2h$$

$$\bar{B}_2 = m - 1/2d + 1/2h$$

Where, m measures the base population mean, d measures the additive gene effects and h measures the dominance gene effects. Weighted least square techniques developed by Fisher (1946), Mather (1949), Scorle (1966) and Mather and Jinks (1971) are followed for the estimation of these parameters (m, d and h). The weight used were the reciprocal of the squared of standard errors of respective generations, as follows -

Weight of $P_1 = 1/(S.E.\bar{P}_1)^2$

Weight of $P_2 = 1/(S.E.\bar{P}_2)^2$

Weight of $F_1 = 1/(S.E.\bar{F}_1)^2$

Weight of $F_2 = 1/(S.E.\bar{F}_2)^2$

Weight of $F_3 = 1/(S.E.\bar{F}_3)^2$

Weight of $B_1 = 1/(S.E.\bar{B}_1)^2$

Weight of $B_2 = 1/(S.E.\bar{B}_2)^2$

By substituting the values of m, d and h in the equations (Equation 1) the expected seven generation means were calculated. The goodness of fit were then tested by squaring the deviations of the observed values from the expected values for each of the seven generations, multiplying by the corresponding weight and then summing the product over all the seven generations. The summed value is the total Chi-square (χ^2) with 4 degrees of freedom.

Therefore, $\chi^2 = \Sigma[(\text{deviation})^2 \times \text{weight}]$

Degree of Freedom(d.f.)= Number of generations minus number of estimates.

The significant chi-square (χ^2) indicates the presence of epistasis which means that additive-dominance model was inadequate due to the presence of non-allelic gene action.

ii) 6-Parameter Model:

When 3-parameter model was not suitable to interpret the gene action owing to epistasis, the data were then subjected to Hayman's (1958) 6-parameter model. The expected generation means in terms of 6-parameter model were as follows -

$$\bar{P}_1 = m + d + i$$

$$\bar{P}_2 = m - d + i$$

$$\bar{F}_1 = m + h + l$$

$$\bar{F}_2 = m + 1/2h + 1/4l$$

$$\bar{F}_3 = m + 1/4h + 1/16l \qquad \text{(Equation 2)}$$

$$\bar{B}_1 = m + 1/2d + 1/2h + 1/4i + 1/4j + 1/4l \quad \text{and}$$

$$\bar{B}_2 = m - 1/2d + 1/2h + 1/4i - 1/4j + 1/4l$$

Where, m measures the base population mean, d measures the additive gene effects, h measures the dominance gene effects, i measures the additive x additive type of non-allelic gene action, j measures the additive x dominance type of non-allelic gene action and l measures the dominance x dominance type of non-allelic gene action.

Weighted least square techniques as described in 3-parameter model were used for the estimation of m, d, h, i, j and l. The weight for each generation was also the same as used in 3-parameter model.

By substituting the value of m, d, h, i, j and l in the equations (Equation 2) the expected generation means were calculated and the goodness of fit was tested by χ^2 in the same way as in the 3-parameter model. In this case there were seven generations and the number of estimates were six, so the degree of freedom (d.f.) was 7 - 6 = 1.

Components of Variation

The variances of segregating generations viz.,F_2, F_3, B_1 and B_2 generations consisted of heritable and non-heritable components. The heritable component consisted of fixable heritable (D) and non-fixable heritable (H) variation. Variations noted in the non-segregating generations (P_1, P_2 and F_1) were non-heritable in nature.

From the seven generations (P_1, P_2, F_1, F_2, F_3, B_1 and B_2) seven different types of variances and covariances were calculated and these were $V\bar{F}_2$, $(V\bar{B}_1 + V\bar{B}_2)$, $V\bar{F}_3$, $\bar{V}F_3$, $W\bar{F}_3/F_2$, VE_1 and VE_2. The composition of these variances in terms of heritable and non-heritable components of variation were as follows :

$$V\bar{F}_2 = 1/2\ D + 1/4\ H + E_1$$

$$(V\bar{B}_1 + V\bar{B}_2) = 1/2D + 1/2H + 2E_1$$

$$V\bar{F}_3 = 1/2\ D + 1/16\ H + E_2$$

$$\bar{V}F_3 = 1/4\ D + 1/8\ H + E_1$$

$$W\bar{F}_3/F_2 = 1/2\ D + 1/8\ H$$

$$VE_1 = E_1$$

$$VE_2 = E_2$$

The non-heritable component of variation in a segregating generation was determined from the variances of non-segregating generations as follows :

$$E_1 = 1/4\ V\bar{P}_1 + 1/4\bar{P}_2 + 1/2V\bar{F}_1$$

E_1 measures the non-heritable variances of the individual. E_2 measures the non-heritable variances of F_3 family means. In general E_2 is less than E_1 because each family mean was based on n number of individuals and E_2 is equal to $(1/n)E_1$. Where the members of all F_3 families are not of equal numbers. E_2 was measured as follows :

$E_2 = E_1/$(Harmonic mean number of plants/F_3 families)

Composition of $V\bar{F}_2$ was determined as follows :

Genotype	Frequency(f)	Effect(e)	f x e	f x $(e)^2$
AA	1/4	+d	1/4(d)	$1/4(d)^2$
Aa	1/2	h	1/2(h)	$1/2(h)^2$
aa	1/4	-d	1/4(-d)	$1/4(-d)^2$
	1	h	1/2 h	$1/2d^2 + 1/2h^2$

Variance of $\bar{F}_2$ $(V\bar{F}_2) = 1/2\ d^2 + 1/2\ h^2 - (1/2\ h)^2$

$= 1/2\ d^2 + 1/2\ h^2 - 1/4\ h^2$

$= 1/2\ d^2 + 1/4\ h^2$

Where there are K gene differences between two parents,

$$V\bar{F}_2 = 1/2\ kd^2 + 1/4\ kh^2$$

Substituting D for kd^2 and H for kh^2,

$$V\bar{F}_2 = 1/2\ D + 1/4\ H$$

Since $V\bar{F}_2$ includes non-heritable variances (E_1) also,

$$V\bar{F}_2 = 1/2\ D + 1/4\ H + E_1$$

In backcross generations B_1 and B_2, there will be two types of genotypes viz., aa and Aa in the B_1 and AA and Aa in the B_2. Thus, the composition of variances of these two generations was determined as follows :

Variance of $\bar{B}_1$ ($V\bar{B}_1$): Where, P_1 = aa

Genotype	Frequency(f)	Effect(e)	f x e	f x $(e)^2$
aa	1/2	-d	1/2(d)	$1/2(-d)^2$
Aa	1/2	h	1/2(h)	$1/(h)^2$
	1	- d + h	- 1/2d + 1/2 h	$1/2d^2 + 1/2h^2$

$$V\bar{B}_1 = 1/2\ d^2 + 1/2\ h^2 - (-\ 1/2d + 1/2h)^2$$

$$= 1/4\ d^2 + 1/4\ h^2 + 1/2\ dh$$

Where there are K gene differences between the two parents,

$$V\bar{B}_1 = 1/4\ kd^2 + 1/4\ kh^2 + 1/2\ kdh$$

Substituting kd^2 and kh^2 for D and H respectively,

$$V\bar{B}_1 = 1/4\ D + 1/4\ H + 1/2\ kdh$$

Variance of $\bar{B}_2$ ($V\bar{B}_2$): Where, P_2 = AA

Genotype	Frequency(f)	Effect(e)	f x e	f x $(e)^2$
AA	1/2	d	1/2(d)	$1/2(d)^2$
Aa	1/2	h	1/2(h)	$1/2(h)^2$
	1	d + h	1/2d + 1/2 h	$1/2d^2 + 1/2h^2$

$$V\bar{B}_2 = 1/2\ d^2 + 1/2\ h^2 - (1/2d + 1/2h)^2$$
$$= 1/4\ d^2 + 1/4\ h^2 - 1/2\ dh$$
$$= 1/2\ d^2 + 1/4\ h^2$$

Where there are K gene differences between the two parents,

$$V\bar{B}_2 = 1/4\ kd^2 + 1/4\ kh^2 - 1/2\ kdh$$

Substituting kd^2 and kh^2 for D and H respectively,

$$V\bar{B}_2 = 1/4\ D + 1/4\ H - 1/2\ kdh$$

Therefore, variances of $\bar{B}_1 + \bar{B}_2$ ($V\bar{B}_1 + V\bar{B}_2$) become,

$$V\bar{B}_1 + V\bar{B}_2 = 1/4D + 1/4H - 1/2kdh + 1/4D + 1/4H - 1/2kdh$$
$$= 1/2D + 1/2H$$

Since, the $V\bar{B}_1$ and $V\bar{B}_2$ involved two independent generations they will include non-heritable variation equal to $2E_1$.

Therefore, $V\bar{B}_1 + V\bar{B}_2$ will be = $1/2D + 1/4H + 2E_1$

In the F_3 generations, all the families derived from AA and aa individuals will be wholly AA and aa respectively, while those individuals from heterozygous F_2 (Aa) will repeat the genotypes like F_2 generations. The means of families from AA, aa and Aa parents will, therefore, be +d, 1/2h and -d in respect of this gene pair. The overall mean thus depart by 1/4h from the mid-parent and the contribution of A-a to the variance of F_3 means will be,

$$V\bar{F}_3 = 1/4d^2 + 1/2(1/2h)^2 + 1/4(-d)^2 - (1/4h)^2$$
$$= 1/2d^2 + 1/16h^2$$

For k genes differences the total heritable variances of F_3 means

will be,

$$V\bar{F}_3 = 1/2kd^2 + 1/16\ h^2$$
$$= 1/2D^2 + 1/16\ H$$

Where, $kd^2 = D$ and $kh^2 = H$

Since $V\bar{F}_3$ calculated from F_3 family means this equation will contain non-heritable variation equal to E_2. Therefore,

$$V\bar{F}_3 = 1/2\ D + 1/16\ H + E_2$$

It can be shown similarly that the mean variances of F_3 families will be,

$$\bar{V}F_3 = 1/4\ d^2 + 1/8\ h^2 + E_1$$
$$= 1/4\ D + 1/8\ H + E_1$$

and the covariances of F_3 means with its F_2 parents measured will be,

$$W\bar{F}_3/F_2 = 1/2\ d^2 + 1/8\ h^2$$
$$= 1/2\ D + 1/8\ H$$

Mean variances of the F_3 families will contain non-heritable components equal to E_1 while covariances will be free from non-heritable effects. Therefore,

$$\bar{V}F_3 = 1/4\ D + 1/8\ H + E_1$$

and $W\bar{F}_3/F_2 = 1/2\ D + 1/8\ H$

The seven equations obtained from the non-segregating and segregating generations were subjected to a least square technique of estimation for the components of variation viz., D, H, E_1 and E_2. An unweighted least square method as developed by Mather (1949) were used. The seven equations obtained were of two

different ranks (rank 1 and rank 2). The components D, H, E_1 and E_2 were estimated including all equations in the least square estimate (rank 1), which was termed as inclusive estimate while these components when estimated excluding $\bar{V}F_3$ statistics was termed as exclusive estimate (rank 2).

However, in order to obtained the estimates of D, H, E_1 and E_2, two steps of calculation were needed. Firstly the C-matrix values were found from the frequencies of D, H, E_1 and E_2 of the equations $V\bar{F}_2$, $V\bar{B}_1 + V\bar{B}_2$, $V\bar{F}_3$, $\bar{V}F_3$, $W\bar{F}_3/F_2$. The C-matrix values obtained are as follows.

Inclusive:

	D	H	E_1	E_2
D	4.19344	-7.79889	0.48357	-0.80464
H	-7.79889	27.72939	-3.49712	1.08318
E_1	0.48357	-3.49712	0.70890	-0.01160
E_2	-0.80464	1.08318	-0.01160	0.66731

Exclusive:

	D	H	E_1	E_2
D	4.62705	-9.34061	0.78920	-0.86486
H	-9.34061	33.21108	-4.58382	1.29731
E_1	0.78920	-4.58382	0.92433	-0.05405
E_2	-0.86486	1.29731	-0.05405	0.67568

The second step was to calculate SDY, SHY, SE_1Y and SE_2

which were calculated as below :

SDY = Coefficient of D (Observed $V\bar{F}_2$ + Observed ($V\bar{B}_1$ + $V\bar{B}_2$) + Observed $V\bar{F}_3$ + Observed $\bar{V}F_3$ + Observed $W\bar{F}_3/F_2$]

SHY = Coefficient of H (Observed $V\bar{F}_2$ + Observed ($V\bar{B}_1$ + $V\bar{B}_2$) + Observed $V\bar{F}_3$ + Observed $\bar{V}F_3$ + Observed $W\bar{F}_3/F_2$]

SE_1Y = Coefficient of E_1 [Observed $V\bar{F}_2$ + Observed ($V\bar{B}_1$ + $V\bar{B}_2$) + Observed $V\bar{F}_3$ + Observed $\bar{V}F_3$ + Observed $W\bar{F}_3/F_2$]

SE_2Y = Coefficient of E_2 [Observed $V\bar{F}_2$ + Observed ($V\bar{B}_1$ + $V\bar{B}_2$) + Observed $V\bar{F}_3$ + Observed $\bar{V}F_3$ + Observed $W\bar{F}_3/F_2$]

The values of SDY, SHY, SE_1Y and SE_2Y and the values of C-matrix analysis were used to determine D, H, E_1 and E_2 (both inclusive and exclusive) of each replication as well as the overall of each character as follows :

$D = SDY \times CDD + SHY \times CDH + SE_1Y \times CDE_1 + SE_2Y \times CDE_2$

$H = SDY \times CDH + SHY \times CHH + SE_1Y \times CHE_1 + SE_2Y \times CHE_2$

$E_1 = SDY \times CDE_1 + SHY \times CHE_1 + SE_1Y \times CE_1E_1 + SE_2Y \times CE_1E_2$

$E_2 = SDY \times CDE_2 + SHY \times CHE_2 + SE_1Y \times CE_1E_2 + SE_2Y \times CE_2E_2$

The components of variation were estimated in the same way as it has been described by Mather (1949), Mather and Vines (1952) and Mather and Jinks (1971).

The least square estimates of components of variation were used to determine the expected variances and covariances of F_2, F_3, B_1 and B_2, generations by adding the frequency of presence of D, H, E_1 and E_2 in each variance and covariance. The least square estimates of D, H, E_1 and E_2 (both inclusive and exclusive) and

the expected variances and covariances were utilized in the further steps of analysis for some genetic studies.

Heritability

The degree to which the variability of a quantitative character may be transmitted to the progeny is referred as heritability. Heritability was calculated in the following ways:

i) Broad Sense Heritability:

It was expressed as the ratio of genotypic variance over the phenotypic variance (expected) of the F_2 generation as follows :

Heritability (Hb) = $(1/2D + 1/4H)/(1/2D + 1/4H + E_1)$

Where D, H and E_1 are the least square estimates of components of variation.

ii) Narrow Sense Heritability:

It was determined as the ratio of fixable heritable variation (D) over the phenotypic variance of F_2 generation as follows :

Heritability (Hn) = $(1/2D)/(1/2D + 1/4H + E_1)$

Where D, H and E_1 are the least square estimates of components of variation.

iii) Parent-offspring regression:

Narrow sense heritability was also estimated by regressing F_3 progeny means on F_2 parental means.

Parent-offspring regression = $(W\bar{F}_3/F_2)/V\bar{F}_2$

Interms of D and H, this heritability becomes,

$= (1/2D + 1/8\ H)/(1/2D + 1/4\ H + E_1)$

Degree of Dominance

i) Potence Ratio Method:

According to Petr and Frey (1966) degree of dominances in F_1, F_2 and F_3 generations were calculated by potence ratio method as follows :

Degree of dominance in $F_1 = h_1 = (\bar{F}_1 - \overline{MP})/(\overline{HP} - \overline{MP})$

Degree of dominance in $F_2 = h_2 = 2(\bar{F}_2 - \overline{MP})/(\overline{HP} - \overline{MP})$

Degree of dominance in $F_3 = h_3 = 4(\bar{F}_3 - \overline{MP})/(\overline{HP} - \overline{MP})$

Where $\overline{MP}$ = Mid-parent value and $\overline{HP}$ = Higher parent value.

ii) Dominance Ratio Method:

The average degree of dominance over all loci was determined by the square root of the ratio between H and D.

Where, $(H/D)^{1/2} = 0$, denotes no dominance.

$(H/D)^{1/2} = 1$, denotes complete dominance.

$(H/D)^{1/2} < 1$, denotes partial dominance

$(H/D)^{1/2} > 1$, denotes over dominance.

Test of Linkage

Whether the genes responsible for different characters were linked or not was tested by following techniques of Mather (1949), Hayman and Mather (1955) and Mather and Jinks (1971).

The test of linkage is also a test of homogeneity of D and H over rank 1 and rank 2 statistics. The sum of deviation square Σ (dev.^{2}) as obtained under inclusive analysis contains variation owing to linkage and residual effects. Whereas the sum of deviation square Σ (dev.^{2}) as obtained under exclusive analysis

contains only residual effects. Therefore, the linkage sum of square was obtained by subtracting exclusive $\Sigma(dev.^2)$ from that of inclusive analysis. These are summarized in the following form:

Item	Sum of squares	Degrees of freedom
Total	$\Sigma(dev.^2)$ from inclusive analysis	3
Residual	$\Sigma(dev.^2)$ from exclusive analysis	2
Linkage	Total S.S. - Residual S.S.	1

Number of Effective Factors

The number of effective factors was estimated in three different ways as follows :

i) Castle and Wright (1921) presented the formula for the estimation of minimum number of factors or genes controlling a character. According to them the possible number of effective gene groups is estimated by dividing the square of difference of the two parental means with the difference of variances of $\bar{F}_2$ and $\bar{F}_1$ multiplied by eight.

Thus, $n_1 = (\bar{P}_1 - \bar{P}_2)^2 / 8(V\bar{F}_2 - V\bar{F}_1)$

ii) According to Mather (1949) the possible number of effective factors is estimated by dividing the square of half of the difference of two parental means with D.

Thus, $K_1 = (1/2\bar{P}_1 - 1/2\bar{P}_2)^2/D$

Where, D is the least square estimate of additive components of genetic variation.

iii) According to Burton (1951) estimation of effective factors

was made as follows :

$$n_2 = [0.25\ (0.75 - h + h^2)\ D^2]/(V\bar{F}_2 - V\bar{F}_1)$$

Where, $D = \bar{P}_2 - \bar{P}_1$ (P_1 always the smaller parent) and

$$h = (\bar{F}_1 - \bar{P}_1)/(\bar{P}_2 - \bar{P}_1)$$

RESULTS

The nine traits of rice studied showed continuous variation indicating polygenic control of these characters. Biometrical techniques of analysis were, therefore, used to determine the nature of gene actions in the expression of these traits.

A. Means and Standard Errors (S.E.)

Means over three replications and standard errors (S.E.) of means of nine characters of different generations are shown in Table-1. The means of all the generations (non-segregating and segregating) were neither greater than the means of higher parent nor less than the means of lower parent. These were within the parental means. The study of means indicated that the hybrids did not show better performance than their better parents in any of the characters studied. The standard errors (S.E.) of each generation of the cross were very low compared to their corresponding means for all the characters as it was expected. Very low standard errors indicated the presence of very low genotype-environment interaction in all the characters.

B. Theoretical Means

Theoretical arithmetic and theoretical geometric means for F_1, F_2, F_3, B_1 and B_2 generations for all the nine characters were estimated and these are summarized in Table-2. Observed means of these generations are also included in the table for comparison. There was a close agreement between the theoretical

arithmetic and theoretical geometric means. The observed means, however, differed from the theoretical arithmetic means and theoretical geometric means in all the generations and characters, except in B_2 in case of primary branches per panicle (Table-2), indicating the involvement of non-additive gene effects in the inheritance of these characters.

In case of plant height the deviations of the observed means from the theoretical arithmetic and theoretical geometric means were very marked in all the generations indicating that non-additive gene effects were operative in all the generations for controlling plant height. The observed mean plant height of F_1 was greater than the theoretical means suggesting the presence of dominance for higher plant height in this cross.

Remarkable differences were noted between the observed means and the theoretical means of effective tillers per plant of F_1, F_2 and F_3 generations indicating non-additive genes were mostly restricted to these generations. Observed F_1 mean was found greater than the theoretical means of this character suggesting dominance for more number of effective tillers per plant was present in the cross.

The deviations between observed means and theoretical means were distinct in panicle length of F_1, B_1 and B_2 generations indicating that non-additive genes for this trait were operative in these generations. The observed F_1 mean was found greater than the theoretical means of panicle length suggested that dominance

for longer panicles in this cross was present.

Distinct differences between the observed means and the theoretical means were noted in flag leaf length of F_1, F_2 and F_3 generations. It suggested that non-additive gene-effects were mostly restricted to these generations. Observed F_1 mean was found greater than the theoretical means of flag leaf length showing the presence of dominance for longer flag leaf length in this cross.

In case of flag leaf breadth, the observed F_1 mean showed difference with the theoretical means and it was greater than these two means. This indicated the involvement of non-additive gene effects restricted in the F_1 generation for this trait and also indicated the presence of dominance for wider flag leaf breadth in the cross.

Well marked differences between the observed means and the theoretical means were noted in all the generations for flag area. This indicated that non-additive gene effects were operative in the trait. The observed F_1 mean was greater than the theoretical means suggesting dominance for larger flag leaf area in this cross.

The deviations between the observed means from the respective theoretical means of F_1 and F_2 generations were distinct in case of primary branches per panicle indicating non-additive gene effects were restricted in these generations. Dominance for more number of primary branches per panicle was

indicated by the greater observed F_1 mean of this traits.

Distinct differences of observed mean from their theoretical means for grains per panicle were marked in all the generations. This suggested that non-additive gene effects were operative in all generations. The observed F_1 mean was found greater than the theoretical means indicating the presence of dominance for higher number of grains per panicle in this cross.

In case of grain yield per plant the deviations of the observed means from the theoretical means were distinct in all the generations indicating the preponderance of non-additive gene effects for the trait. The observed F_1 mean was also found greater than the corresponding theoretical means suggesting the presence of dominance for higher grain yield per plant in this cross.

C. Scaling Test

The types of gene action involved in the mean expression of different characters were determined by Mather's A, B, C and D Scaling Test (1949). A, B, C and D related to B_1, B_2, F_2 and F_3 generations, respectively, were estimated to test the significant deviations of the observed means of B_1, B_2,F_2 and F_3 generations from their expectations and these are presented in Table-3. The significance of the items suggested that non-additive gene action had affected the means of these segregating generations.

All the four items of the nine characters studied were found positive except the item A in case of flag leaf length where it

was negative in nature. From Table-3 it was observed that the items A, C and D in plant height; C and D in effective tillers per plant and flag leaf length; A and D in panicle length and grain yield per plant; A in flag leaf breadth; A and C in flag leaf area and all the items in grains per panicle were significant. All these significant deviations from their expectations for all the characters, except primary branches per panicle, of the cross suggested non-allelic gene action was involved in the inheritance of these characters. In case of primary branches per panicle, all the items other than B were non-significant and the estimate B was equal to zero. This indicated the presence of epistasis but non-significantly in B_1, F_2 and F_3 generations and epistasis did not affect the mean of B_2 generation in case of primary branches per panicle.

D. Epistatic Gene Effect

1) 3-Parameter Model :

The data of nine characters were analysed in terms of 3-parameter model according to Hayman (1958) to determine the type of gene action. The weighted least square estimates of m, d and h of all the characters were calculated separately and the results are summarized in Table-4. χ^2 test was made to test the goodness of fit of the observed generation means. The $\chi^2_{(df=4)}$ values are also included in Table-4. Significant χ^2 values indicated that epistasis was involved in controlling the different generation means of the cross. The additive-dominance

model was, however, adequate in those cases where the χ^2 values were non-significant and the interpretation of the result in terms of 3-parameter model would be valid in those cases. Significant χ^2 values were observed in all the cases except in case of flag leaf area and primary branches per panicle. The magnitude of estimates of mean effect (m) were found higher than those of additive gene effects (d) and dominance gene effects (h) and values of m were highly significant in all the characters studied. The estimates of additive gene effect (d) in all characters were found negative. Except the case of flag leaf breadth, the magnitude of d was found larger than that of dominance effect (h) and these d effects were found highly significant. The dominance gene effect (h) was found significant and positive in nature in all the characters studied.

The estimates of m, d and h from 3-parameter model will be biased to an unknown extent by effects not attributable to the additive and dominance action of genes in those case where χ^2 values were significant.

ii) 6-parameter Model :

As the $\chi^2_{(df=4)}$ estimates under the 3-parameter model were significant, the data were analysed in terms of 6-parameter model to separate the epistatic gene effects from the m, d and h. The weighted least square estimates for m, d, h, i, j and l in terms of 6-parameter model were calculated and the results are presented in Table-5. Here, m measures the mean effect, d and h

measure the algebraic sum of additive and dominance effects respectively and i, j and l measure the algebraic sum of epistatic effects, additive x additive (i), additive x dominance (j) and dominance x dominance (l) types of gene interaction respectively. The χ^2 test was then made to test the goodness of fit of the observed generation means with the expected means. The $\chi^2_{(df=1)}$ was found non-significant in all the cases. Thus, in these cases the 6-parameter model was adequate and the estimates of d and h and the interaction items were interpretable.

The estimates of mean effect (m) were found highly significant and positive in all the cases and were usually greater in magnitude compared to the other estimates. All the estimates of additive gene effect (d) were also found highly significant but these effects were negative in nature (Table-5). All the d estimates, except the case of flag leaf area, were larger in magnitude than the h estimates of the respective characters. All the dominance effects (h), except the cases of effective tillers per plant and flag leaf length, were positive, low and non-significant. In case of effective tillers per plant and flag leaf length, the h estimates were also low and non-significant but these were negative in nature.

The estimates of epistatic gene effects (i, j and l) showed that the magnitude of all the epistatic effects in all the traits, except the case of flag leaf breadth, were less than the

mean effects (m) and dominance effects (d). The additive x additive (i) epistasis were found to be negative in nature except the case of flag leaf breadth where it was positive. The estimates of i epistasis were observed to be significant in cases of plant height, effective tillers per plant, flag leaf length, flag leaf breadth and grains per panicle (Table-5). In case of additive x dominance epistasis both positive and negative types of j estimates were also observed. The j estimates of effective tillers per plant and grains per panicle were negative while those of the other characters were positive in nature. However, significant j estimates were observed only in case of plant height and flag leaf breadth (Table-5). The dominance x dominance type of epistasis, l estimates were found both positive and negative in nature but all the estimates were non-significant.

In all the traits, except in case of primary branches per panicle, opposite signs of 'h' and 'l' were observed indicating the presence of duplicate type of gene action in these cases. In case of primary branches per panicle, the signs of 'h' and 'l' were same suggesting that the interactions were on balance and were of mainly complementary type.

E. Components of Variation

The unweighted least square estimates of components of variation (D, H, E_1 and E_2) were measured both under inclusive and exclusive analysis and the results are summarized in Table-6.

D represents the additive variation, H represents the dominance variation and E_1 and E_2 represent environmental variation.

i) Inclusive Analysis :

From the results, it was observed that the estimates of D of all the characters were larger in magnitude than the other estimates (H, E_1 and E_2). It was also observed that all the estimates of D were positive and significant (Table-6). Significant estimates of D with greater magnitude found in all the characters revealed that additivity played an important role in the inheritance of these characters. The estimates of H for all the characters were found negative and non-significant. In all the cases the estimates of E_1 were found very low, positive and insignificant. Insignificant low estimates of E_2 were also observed in all the case. Estimates of E_2 were found positive except in cases of plant height and primary branches per panicle.

ii) Exclusive Analysis :

From Table-6 it was revealed that more or less similar results like inclusive analysis were obtained during the estimation of components of variation by exclusive analysis. In all the characters the estimates of D were larger in magnitude than the other estimates (H, E_1 and E_2). All the estimates of D were found positive and significant except in case of flag leaf area where it was found non-significant (Table-6). Large and significant estimates of D indicated that additive genes were of more importance than the other estimates in the inheritance of

these characters. In case of H, all the estimates were found negative and non-significant. Insignificant estimates of E_1 and E_2 were also obtained in all the cases. These estimates were very lower in magnitude compared to the estimates of D and H and were positive in nature except the cases of plant height and primary branches per panicle.

F. Heritability

Heritability estimates, both broad sense (Hb) and narrow sense (Hn), based on the components of variation as well as on the basis of parent-offspring regression, were determined in percentage for all the characters and these estimates are shown in Table-7.

Estimates of broad sense heritability (Hb) in both the analysis (inclusive and exclusive) were high in majority of the characters. Inclusive estimates of broad sense heritability ranged from 41.27% in panicle length to 80.24% in grain yield per plant (Table-7). The inclusive estimate of broad sense heritability of grain yield per plant was followed by the estimates of grains per panicle (80.20%) and flag leaf length (80.08%). Moderate inclusive estimates of broad sense heritability were observed in effective tillers per plant (41.44%) and panicle length (41.27%). Exclusive analysis of broad sense heritability estimates gave more or less similar results for all the traits. These estimates ranged from 37.12% in panicle length to 77.17% in grain yield per plant.

Estimates of narrow sense heritability (Hn), obtained from both the analysis, were also found high in all the cases. The estimates varied with wide ranges in both the analysis. In case of inclusive analysis the range was 98.18% to 143.19 (Table-7). The highest percent of narrow sense heritability estimate was observed in plant height (143.19%) followed by flag leaf breadth (120.23%) and primary branches per panicle (115.80%). The lowest percent of the estimate was observed in panicle length (98.18%). More or less similar results for all the characters were obtained in the exclusive analysis. Here the narrow sense heritability ranged from 99.71% in panicle length to 143.54% in plant height.

High heritability estimates for all the traits were also obtained from parent-offspring regression analysis. The estimates ranged 68.42% in panicle length to 108.33% in plant height (Table-7).

High estimates of heritability indicated that most of the variations were of genetic in nature.

G. Degree of dominance

1) Potence Ratio Method :

Degrees of dominance (h_1, h_2 and h_3 related F_1, F_2 and F_3 generations, respectively) for the nine characters were estimated separately by potence ratio method and the results are presented in Table-8. All the characters of F_1 and F_2 generations showed partial dominance, except the case of flag leaf length in F_2 which showed over dominance. On the other hand in F_3 most of

characters, except panicle length, flag leaf breadth and grain yield per plant, showed overdominance. While panicle length, flag leaf breadth and grain yield per plant in F_3 showed partial dominance. The range of dominance values were 0.29 to 0.59, 0.45 to 1.13 and 0.91 to 2.22 in F_1, F_2 and F_3 generations, respectively. However, all the dominance were positive in nature.

ii) Dominance Ratio Method:

The H estimates during both inclusive and exclusive estimation yielded non-significant negative values in all cases indicating the absence of dominance gene effect. Negative H estimates of components of variation, however, arose from the sampling errors or due to genotype-environment interaction. Such H values are to be considered as zero. Thus, considering the H estimates as zero, all the estimates of degree of dominance obtained by dominance ratio method $(H/D)^{1/2}$ were found to be zero i.e. no dominance was detected in all the traits and these estimates (zero values) are not included in the dominance table (Table-8).

H. Test of Linkage

In order to test the linkage, the expected variances and covariances of F_2, F_3, B_1 and B_2 generations and also the environmental variances present in them were calculated (both inclusive and exclusive) from the components of variation for different characters. The results are summarized in Table-9. The observed variances and covariances of the segregating generations

and the observed environmental variances of them are also included in Table-9. However, if the linkage was present then D and H of rank 2 statistics (excluding $\bar{V}F_3$ when the other variances and covariances are used) would differ from D and H of rank 1 statistics (when all the variances and covariances are used). The next step was to calculate the linkage variances for different characters with the help of variances and covariances of Table-9. The results from the analysis of variance to test the effect of linkage for different characters are presented in Table-10. The item linkage (df=1) was tested with the item residual (df=2) and it was found that in all the cases the linkage item was non-significant.

I. Number of Effective Factors

The number of effective factors for different characters were calculated in three different way following the methods of Castle and Wright, 1921 (n_1); Burton, 1951 (n_2) and Mather, 1949 (K_1) and the results are shown in Table-11.

According to Castle and Wright's method (1921) more than one effective factors were detected to control the nine characters studied in the cross. The number of effective factors (n_1) for controlling these characters ranged from 2 to 22 (Table-11). At least 2 pairs of gene groups were responsible for controlling flag leaf length, flag leaf breadth , flag leaf area and primary branches per panicle. At least 3 pairs of effective factors were involved in controlling plant height and panicle length. More

than 5 and 7 pairs of gene groups were detected for grain yield per plant and effective tillers per plant, respectively. However, the highest number of effective factors, at least 22 pairs of gene group, was detected in grains per panicle responsible for controlling the trait.

Similar results were obtained by Burton's method in detecting the number of effective factors (n_2) except grains per panicle. In this case at least 23 pairs of gene groups was estimated responsible for controlling this traits (Table-11).

Mather's method in detecting number of effective factor's (K_1) also resulted more or less similar numbers of gene pairs responsible for controlling these characters. At least 2 pairs of gene groups for flag leaf length, flag leaf breadth and primary branches per panicle; 3 pairs for plant height, panicle length and flag leaf area; 7 pairs for grain yield per plant; 9 pairs for effective tillers per plant and 26 pairs for grains per panicle were detected responsible for controlling these characters (Table-11).

Table-1

Means and standard errors of different characters for different generations.

Generations	Plant height (cm)	Effective tillers/ plant	Panicle length (cm)	Flag leaf length (cm)	Flag leaf breadth (cm)
P_1	87.00 ±1.05	5.63 ±0.15	25.40 ±0.25	30.90 ±0.35	1.350 ±0.021
P_2	137.00 ±1.20	9.67 ±0.15	28.90 ±0.26	38.80 ±0.39	1.683 ±0.022
F_1	123.50 ±1.57	8.27 ±0.23	27.66 ±0.41	37.20 ±0.39	1.580 ±0.033
F_2	124.30 ±1.75	8.18 ±0.09	27.56 ±0.15	37.08 ±0.40	1.564 ±0.013
F_3	124.40 ±1.41	8.23 ±0.07	27.55 ±0.12	37.04 ±0.35	1.545 ±0.010
B_1	113.60 ±2.09	7.00 ±0.18	27.00 ±0.32	33.94 ±0.84	1.503 ±0.027
B_2	132.50 ±2.06	9.03 ±0.18	28.70 ±0.31	37.80 ±0.75	1.667 ±0.025

Continued to overleaf

Table-1 (Continued)

Means and standard errors of different characters for different generations.

Generations	Flage leaf area (sq.cm.)	Primary branches/ panicle	Grains/ panicle	Grain yield/ plant (gm)
P_1	32.89 ±0.47	10.10 ±0.25	93.87 ±1.40	10.84 ±0.29
P_2	44.67 ±0.52	12.93 ±0.26	230.10 ±1.54	24.64 ±0.32
F_1	41.27 ±0.53	12.27 ±0.40	182.80 ±1.56	20.79 ±0.32
F_2	40.89 ±0.63	12.03 ±0.23	184.86 ±1.59	19.68 ±0.33
F_3	40.45 ±0.52	11.96 ±0.18	185.21 ±1.42	19.39 ±0.29
B_1	38.99 ±0.97	11.37 ±0.35	147.80 ±3.33	17.79 ±0.69
B_2	43.81 ±0.83	12.60 ±0.31	216.10 ±2.97	23.20 ±0.62

Table-2

Observed means, theoretical arithmetic means and theoretical geometric means (1st, 2nd and 3rd values of a group, respectively) of F_1, F_2, F_3, B_1 and B_2 generations.

Generations	Plant height (cm)	Effective tillers/ plant	Panicle length (cm)	Flag leaf length (cm)	Flag leaf breadth (cm)
F_1	123.50	8.27	27.66	37.20	1.580
	112.00	7.65	27.15	34.85	1.517
	109.17	7.38	27.09	34.63	1.507
F_2	124.30	8.18	27.56	37.08	1.564
	117.75	7.96	27.41	36.03	1.548
	116.12	7.81	27.38	35.89	1.535
F_3	124.40	8.23	27.55	37.04	1.545
	118.15	7.92	27.36	35.97	1.540
	116.49	7.77	27.33	35.83	1.535
B_1	113.60	7.00	27.00	33.94	1.503
	105.25	6.95	26.53	34.05	1.465
	103.66	6.82	26.51	33.90	1.460
B_2	132.50	9.03	28.70	37.80	1.667
	130.25	8.97	28.28	38.00	1.632
	130.07	8.94	28.27	37.99	1.631

Continued overleaf

Table-2 (Continued)

Observed means, theoretical arithmetic means and theoretical geometric means (1st, 2nd and 3rd values of a group, respectively) of F_1, F_2, F_3, B_1 and B_2 generations.

Generations	Flage leaf area (sq.cm.)	Primary branches/ panicle	Grains/ panicle	Grain yield/ plant (gm)
F_1	41.27	12.27	182.80	20.79
	38.78	11.52	161.99	17.74
	38.33	11.43	146.97	16.34
F_2	40.89	12.03	184.86	19.68
	40.03	11.89	172.39	19.27
	39.77	11.84	163.91	18.43
F_3	40.45	11.96	185.21	19.39
	39.84	11.77	173.42	18.71
	39.59	11.72	164.83	17.93
B_1	38.99	11.37	147.80	17.79
	37.08	11.19	138.34	15.82
	36.84	11.13	130.99	15.01
B_2	43.81	12.60	216.10	23.20
	42.97	12.60	206.45	22.72
	42.94	12.60	205.09	22.63

Table-3

Mather's A, B, C and D scaling test related to B_1, B_2, F_2 and F_3 generations respectively for different characters.

	Plant height	Effective tillers/ plant	Panicle length	Flag leaf length	Flag leaf breadth
A	16.70 ±2.65	0.10 ±0.27	0.94 ±0.46	-0.22 ±1.02	0.076 ±0.038
B	4.50 ±2.64	0.12 ±0.26	0.84 ±0.45	-0.40 ±0.92	0.071 ±0.037
C	26.20 ±4.52	0.88 ±0.36	0.62 ±0.63	4.22 ±1.08	0.063 ±0.051
D	25.00 ±3.93	1.26 ±0.22	0.78 ±0.39	4.30 ±0.99	0.019 ±0.032

	Flage leaf area (sq.cm.)	Primary branches/ panicle	Grains/ panicle	Grain yield/ plant (gm)
A	3.82 ±1.19	0.37 ±0.48	18.93 ±4.04	3.95 ±0.84
B	1.68 ±1.04	0 ±0.45	19.30 ±3.65	0.97 ±0.76
C	3.46 ±1.64	0.55 ±0.74	49.87 ±4.27	1.66 ±0.89
D	2.46 ±1.47	0.75 ±0.54	47.15 ±3.94	2.72 ±0.82

Table-4

Estimates of m, d and h based on 3-parameter model and χ^2 testing the heterogeneity of observed means from that of expected based on 3-parameter model for different characters.

	m	d	h	$\chi^2_{(df=4)}$
Plant height	113.80±0.72	-24.80±0.77	15.23±1.63	49.13***
Effective tillers/plant	7.91±0.08	-2.00±0.10	0.58±0.20	16.08**
Panicle length	27.57±0.14	-1.71±0.17	0.70±0.35	15.45**
Flag leaf length	35.35±0.22	-3.98±0.25	2.32±0.46	18.46***
Flag leaf breadth	1.568±0.011	-0.014±0.015	0.257±0.029	411.00***
Flag leaf area	39.17±0.31	-5.86±0.34	2.68±0.62	6.49*
Primary branches/ panicle	11.62±0.15	-1.39±0.17	0.80±0.37	1.26
Grains/panicle	168.23±0.89	-73.61±1.01	21.58±1.81	161.99***
Grain yield/ plant	18.06±0.19	-6.86±0.21	3.13±0.38	12.67*

*, ** and *** = Significant at 5%, 1% and 0.1% level, respectively.

Table-5

Estimates of m, d and h and the three types of gene interaction (i, j, and l) based on 6-parameter model and χ_2 testing the heterogenity of observed means from that of the expected based on 6-parameter model for different characters.

	m	d	h	i	j	l	$\chi^2_{(df=1)}$
Plant height	122.11 ±3.18	-24.99 ±0.80	10.69 ±10.77	-10.07 ±3.21	12.27 ±6.04	-9.28 ±8.45	0.34
Effective tillers/plant	8.35 ±2.00	-2.00 ±0.11	-0.51 ±0.82	-0.65 ±0.21	-0.01 ±0.55	0.48 ±0.78	0.83
Panicle length	27.22 ±0.35	-1.73 ±0.18	1.53 ±1.43	-0.02 ±0.37	0.11 ±0.96	-1.08 ±1.36	1.56
Flag leaf length	37.66 ±0.93	-3.93 ±0.26	-2.83 ±3.39	-2.83 ±0.95	0.19 ±2.31	2.33 ±2.65	0.67
Flag leaf breadth	1.557 ±0.011	-0.080 ±0.015	0.221 ±0.118	0.392 ±0.031	0.269 ±0.079	0.011 ±0.112	3.48
Flag leaf area	39.02 ±1.27	-5.88 ±0.35	6.37 ±4.46	-0.21 ±1.29	1.93 ±2.64	-4.19 ±3.46	0.44
Primary branches/ panicle	11.87 ±0.46	-1.41 ±0.18	0.37 ±1.69	-0.33 ±0.47	0.36 ±0.99	0.02 ±1.49	0.02
Grains/panicle	185.51 ±3.90	-68.05 ±1.04	1.41 ±14.24	-23.40 ±3.98	-1.93 ±9.06	-4.73 ±11.05	1.78
Grain yield/ plant	18.12 ±0.77	-6.89 ±0.22	5.14 ±2.82	-0.36 ±0.79	2.76 ±1.90	-2.49 ±2.20	2.79

Table-6

Least square estimates of the components of variation D, H, E_1 and E_2 and their respective standard erreors of different characters (the upper and lower values of a pair represent the inclusive and exclusive estimates of components of variation).

	D	H	E_1	E_2
Plant height	227.37±102.59	-208.09±263.81	17.73±42.18	-4.91±40.92
	233.20±105.06	-228.79±281.46	21.83±46.96	-5.71±40.15
Effective tillers/plant	0.458±0.221	-0.531±0.567	0.136±0.091	0.023±0.088
	0.476±0.227	-0.594±0.609	0.148±0.102	0.020±0.087
Panicle length	1.373±0.657	-1.592±1.689	0.411±0.270	0.075±0.262
	1.430±0.678	-1.796±1.815	0.451±0.303	0.067±0.259
Flag leaf length	11.305±4.125	-6.350±10.607	1.011±1.696	0.246±1.646
	11.546±4.298	-7.206±11.515	1.180±1.921	0.212±1.643
Flag leaf breadth	0.0094±0.0045	-0.0108±0.0115	0.0028±0.0018	0.0005±0.0018
	0.0098±0.0047	-0.0122±0.0126	0.0030±0.0021	0.0004±0.0018
Flag leaf area	27.092±13.901	-22.255±35.747	2.398±5.716	0.253±5.545
	28.230±14.363	-26.301±38.481	3.200±6.420	0.095±5.489
Primary branches/ panicle	3.938±1.641	-4.684±4.220	0.674±0.675	-0.019±0.655
	3.864±1.712	-4.362±4.586	0.611±0.765	-0.006±0.654
Grains/panicle	179.09±64.44	-102.40±165.72	15.79±26.50	4.78±25.71
	183.02±67.08	-116.39±179.72	18.57±29.98	4.23±25.63
Grain yield/plant	7.759±2.776	-4.441±7.139	0.682±1.141	0.201±1.107
	7.926±2.890	-5.035±7.744	0.800±1.292	0.178±1.105

Table-7

Heritability estimates in percentage of different characters.

	Hb		Hn		P/O
	Inclusive	Exclusive	Inclusive	Exclusive	
Plant height	77.67	73.13	143.19	143.54	108.33
Effective tillers/plant	41.44	37.68	98.60	100.21	68.95
Panicle length	41.27	37.12	98.18	99.71	68.42
Flag leaf length	80.08	77.09	111.36	112.06	94.58
Flag leaf breadth	71.85	63.32	120.23	122.64	92.98
Flag leaf area	79.29	69.96	98.76	101.50	85.73
Primary branches/panicle	64.02	54.44	115.80	117.98	86.21
Grains/ panicle	80.20	77.07	112.30	113.00	95.03
Grain yield/ plant	80.24	77.17	112.41	113.09	95.13

Hb = Broad sense heritability
Hn = Narrow sense heritability
P/O = Parent offspring regression
(Calculated from the exclusive estimates)

Table-8

Degree of dominance based on potence ratio (h_1, h_2 and h_3) method of different characters.

	h_1	h_2	h_3
Plant height	0.46	0.98	1.98
Effective tillers/plant	0.31	0.52	1.15
Panicle length	0.29	0.45	0.91
Flag leaf length	0.59	1.13	2.22
Flag leaf breadth	0.38	0.57	0.68
Flag leaf area	0.42	0.72	1.13
Primary branches/panicle	0.53	0.73	1.26
Grains/panicle	0.31	0.67	1.36
Grain yield/plant	0.44	0.56	0.96

Table-9

Inclusive and exclusive estimates of variances and covariances of different characters. The first and second value of a pair are the observed and expected estimates, respectively.

Statistics	Inclusive	Exclusive	Inclusive	Exclusive
	Plant height		Effective tillers/plant	
$V\bar{F}_2$	137.52 79.39	137.52 81.23	0.360 0.232	0.360 0.238
$V\bar{B}_1+V\bar{B}_2$	25.84 49.10	25.84 45.87	0.195 0.236	0.195 0.237
$V\bar{F}_3$	89.00 95.78	89.00 96.58	0.205 0.219	0.205 0.221
$\bar{V}F_3$	41.08 48.56	- -	0.161 0.184	- -
$W\bar{F}_3/F_2$	59.32 87.68	59.32 88.00	0.103 0.163	0.103 0.164
VE_1	5.60 17.73	5.60 21.83	0.113 0.136	0.113 0.148
VE_2	1.87 -4.91	1.87 -5.71	0.038 0.023	0.038 0.020

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Table-9 (Continued)

Inclusive and exclusive estimates of variances and covariances of different characters. The first and second value of a pair are the observed and expected estimates, respectively.

Statistics	Inclusive	Exclusive	Inclusive	Exclusive
	Panicle length		Flag leaf length	
$V\bar{F}_2$	1.080 0.699	1.080 0.717	7.306 5.076	7.306 5.151
$V\bar{B}_1+V\bar{B}_2$	0.590 0.712	0.590 0.719	3.822 4.500	3.822 4.530
$V\bar{F}_3$	0.622 0.662	0.622 0.670	5.600 5.502	5.600 5.535
$\bar{V}F_3$	0.482 0.555	- -	2.740 3.044	- -
$W\bar{F}_3/F_2$	0.306 0.488	0.306 0.491	3.360 4.859	3.360 4.872
VE_1	0.347 0.411	0.347 0.451	0.439 1.011	0.439 1.180
VE_2	0.116 0.075	0.116 0.067	0.146 0.246	0.146 0.212

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Table-9 (Continued)

Inclusive and exclusive estimates of variances and covariances of different characters. The first and second value of a pair are the observed and expected estimates, respectively.

Statistics	Inclusive	Exclusive	Inclusive	Exclusive
	Flag leaf breadth		Flag leaf area	
$V\bar{F}_2$	0.0074 0.0048	0.0074 0.0049	18.135 10.380	18.135 10.740
$V\bar{B}_1+V\bar{B}_2$	0.0040 0.0048	0.0040 0.0049	4.871 7.214	4.871 7.365
$V\bar{F}_3$	0.0042 0.0045	0.0042 0.0046	12.397 12.408	12.397 12.566
$\bar{V}F_3$	0.0033 0.0038	- -	4.927 6.380	- -
$W\bar{F}_3/F_2$	0.0021 0.0033	0.0021 0.0034	6.094 10.764	6.094 10.827
VE_1	0.0023 0.0028	0.0023 0.0030	0.791 2.398	0.791 3.200
VE_2	0.0008 0.0005	0.0008 0.0004	0.264 0.253	0.264 0.095

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Table-9 (Continued)

Inclusive and exclusive estimates of variances and covariances of different characters. The first and second value of a pair are the observed and expected estimates, respectively.

Statistics	Inclusive	Exclusive	Inclusive	Exclusive
	Primary branches/panicle		Grains/panicle	
$V\bar{F}_2$	2.360	2.360	114.08	114.08
	1.472	1.453	79.74	80.98
$V\bar{B}_1+V\bar{B}_2$	0.634	0.639	59.73	59.73
	0.975	0.973	69.93	70.46
$V\bar{F}_3$	1.523	1.523	90.38	90.38
	1.657	1.653	87.92	88.47
$\bar{V}F_3$	1.185	-	42.71	-
	1.073	-	47.76	-
$W\bar{F}_3/F_2$	0.908	0.908	52.65	52.65
	1.383	1.387	76.75	76.96
VE_1	0.345	0.345	6.89	6.89
	0.674	0.611	15.79	18.57
VE_2	0.115	0.115	2.30	2.30
	-0.190	-0.006	4.78	4.23

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Table-9 (Continued)

Inclusive and exclusive estimates of variances and covariances of different characters. The first and second value of a pair are the observed and expected estimates, respectively.

Statistics	Inclusive	Exclusive
	Grain yield/plant	
$V\bar{F}_2$	4.933 3.451	4.933 3.504
$V\bar{B}_1+V\bar{B}_2$	2.582 3.023	2.582 3.046
$V\bar{F}_3$	3.905 3.803	3.905 3.826
$\bar{V}F_3$	1.852 2.067	- -
$W\bar{F}_3/F_2$	2.289 3.324	2.289 3.334
VE_1	0.298 0.682	0.298 0.800
VE_2	0.099 0.201	0.099 0.178

Table-10

Results of analysis of variance for the test of linkage for different characters.

Item		SS	DF	MS	VR
Plant height	Linkage	248.82	1	248.82	0.10
	Residual	4770.63	2	2385.32	
	Total	5019.45	3		
Effectiv tillers/ plant	Linkage	0.0009	1	0.0009	0.08
	Residual	0.0223	2	0.0112	
	Total	0.0232	3		
Panicle length	Linkage	0.0074	1	0.0074	0.07
	Residual	0.1984	2	0.0992	
	Total	0.2058	3		
Flag leaf length	Linkage	0.1295	1	0.1295	0.03
	Residual	7.9856	2	3.9928	
	Total	8.1151	3		
Flag leaf breadth	Linkage	1.000002	1	0.000002	0.07
	Residual	0.000056	2	0.000028	
	Total	0.000058	3		
Flag leaf area	Linkage	3.38	1	3.38	0.23
	Residual	28.91	2	14.46	
	Total	32.29	3		
Primary branches/ panicle	Linkage	0.0375	1	0.0375	0.20
	Residual	0.3793	2	0.1897	
	Total	0.4168	3		
Grains/panicle	Linkage	35.67	1	35.67	0.04
	Residual	1945.10	2	972.55	
	Total	1980.77	3		
Grain yield/plant	Linkage	0.0646	1	0.1646	0.04
	Residual	3.6111	2	1.8056	
	Total	3.6757	3		

Table-11

Estimates of number of effective factors (n_1, n_2 and K_1).

	n_1	n_2	K_1
Plant height	2.40	2.66	2.68
Effective tillers/ plant	7.26	7.61	8.57
Panicle length	2.61	2.72	2.14
Flag leaf length	1.14	1.34	1.35
Flag leaf breadth	1.04	1.12	1.30
Flag leaf area	1.58	1.72	2.07
Primary branches/ panicle	1.06	1.11	1.08
Grains/panicle	21.73	22.74	25.35
Grain yield/plant	5.16	5.66	6.01

DISCUSSION

Inheritance of nine quantitative characters of rice (*Oryza sativa* L.) was studied in a single cross involving two rice mutant lines. The nine studied characters were plant height, effective tillers/plant, panicle length, flag leaf length, flag leaf breadth, flag leaf area, primary branches per panicle, grains per panicle and grain yield per plant. The biometrical techniques of analysis developed by Mather (1949) based on the mathematical models of Fisher *et al.* (1932) and those of Hayman (1958) and Allard (1960) were followed for studying the inheritance of these nine characters. All the characters showed continuous variations in them and followed the normal distribution in every case. The inheritance of these quantitative characters were studied on the basis of some important assumptions proposed by Mather (1949) and Anderson and Kempthorne (1954). These are (a) multiple alleles absent, (b) linkage absent, (c) lethal gene absent, (d) constant variability for all the genotypes and (e) environmental effects additive with the genotypic value. Assumptions a, b and c would be no serious bias in the estimation of the parameters. The parental lines taken for the study were pure homozygous, as these lines have been maintained through selfing for many generations since 1975, due to which multiple allele and lethal genes were not likely to be present in the cross. The variability was expected to be constant

for all the genotypes and no bias would be expected. The presence of linkage among the genes may cause important bias in the estimates. Only early generations are considered in this study and as equilibrium of linkage relations is improbable (Comstock and Robinson, 1952 and Mather, 1949), therefore, if there is epistasis, bias due to linkage relations would be present in the estimates of gene effects (Kempthorne, 1957). The most serious bias would be expected to occur in the estimates of additive x additive (i) and dominance x dominance (l) effects.

The effects of environments on genotypes were noted in several crops (Rajas and Sprague, 1952; Perkins and Jinks, 1968; Busch *et al.*, 1976 and Uddin *et al.*, 1979 and 1980). In this study, the bias due to genotype-environment interaction was less as the standard errors of each generation were low. Inclusion of different years and locations, if possible, gave an estimate of different parameters free from genotype-environment interaction.

Estimates of means showed that the means of segregating generations (F_2, F_3, B_1 and B_2) and non-segregating generation (F_1) were within the parental ranges i.e., did not exceeded the parental means in all the cases.

The observed means of F_1, F_2, F_3, B_1 and B_2 generations differed from those of theoretical arithmetic and theoretical geometric means in most of the cases suggesting the involvement of non-additive and non-allelic gene effects in the inheritance of these characters. Allard and Harding (1963), Bitzer *et al.*

(1971), Busch *et al.* (1976), Jatasra and Paroda (1978) and Gill *et al.* (1979) reported the preponderance of non-additive gene action in the inheritance of some agronomic characters of wheat. They also noted the presence of additive type of gene actions. Domiannce towards better performances of the nine characters were observed. Dominance towards better performance of different agronomic traits have been reported by many investigators such as Li and Chang (1970), Ali *et al.* (1975), Singh and Nanda (1976), Shaalai and Aly (1977) and Kumar *et al.* (1986).

Mather's A, B, C and D Scaling Test related to B_1, B_2, F_2 and F_3 generations respectively were made to test the significant deviations of the observed means from their expectations. Significant deviations of the observed means from their expectations were found for all the characters in most of the tests suggesting the presence of non-additive and non-allelic gene action in the inheritance of these characters.

As A, B, C and D scaling test is specific to B_1, B_2, F_2 and F_3 generations respectively, a Joint Scaling Test (Cavalli, 1952) allowing all the seven generations together was done for testing the adequacy of additive-dominance model ($\chi^2_{df=4}$). Significant $\chi^2_{(df=4)}$ values indicated the presence of epistasis (non-allelic gene actions) while non-significant χ^2 values suggested the gene actions free from non-allelic interactions. Significant χ^2 values were observed in plant height, effective tillers per plant, panicle length, flag leaf length, flag leaf breadth, grains per

panicle and grain yield per plant suggesting the presence of non-allelic gene action. The other two characters viz., flag leaf area and primary branches per panicle showed non-significant χ^2 values indicating the gene actions free from non-allelic interactions. But Mather's Scaling Tests were significant in these two cases indicating the presence of non-additive and non-allelic gene interactions. Linkage and higher order gene interaction may cause non-significant χ^2 estimates in these two cases. Allard (1960), Bitzer *et al.* (1971) and Busch *et al.* (1976) in wheat and Kumar *et al.* (1986), Hahn and Chae (1987) and Choi (1990) in rice found non-additive and non-allelic gene interactions for different agronomic traits.

The digenic interaction model ($\chi^2_{df=1}$) was used as the additive-dominance model ($\chi^2_{df=4}$) was inadequate in this cross. Non-significant $\chi^2_{(df=1)}$ values were found in all the characters indicating that digenic interaction model was adequate in these cases. Weighted estimates of additive, dominance and digenic interaction parameters were calculated as proposed by Hayman (1958). The estimates were meaningful in all the cases as all the χ^2 values with 1 df were non-significant. Additive gene effects (d) were significant in all the traits studied suggested that additive gene effects made the major contribution to the variation of all the cases. The sign of d estimate is not important as it depends on the parental means [$d=(\bar{P}_1-\bar{P}_2)/2$]. On the other hand the estimates of dominance (h) effects of all the

characters were found non-significant. Though the h estimates of flag leaf breadth, flag leaf area and grain yield per plant were non-significant, these estimates were positive and large compared to their respective errors indicating dominance towards larger flag leaf breadth and area and towards more grain yield. However, the d as the additive (d) estimates of all the characters were significant and larger than the dominance (h) estimates, it was revealed that the additive (d) effects contributed major part in the inheritance of these characters. Gill *et al.* (1979) in macaroni wheat and Hahn and Chae (1987) in rice have reported major contribution of additive effects in the inheritance of some important agronomic traits. Kumar *et al.* (1986) while studying some crosses using rice dwarf mutants found that plant height was governed predominantly by additive genes with dominance gene action.

The estimates of epistatic gene effects (i, j and l) showed that the total epistatic effects varied in different characters and were less than the mean effects (m). Additive x additive (i) types of epistasis were more pronounced than additive x dominance (j) and dominance x dominance (l) types of epistasis. Additive x additive (i) types of epistasis were found significant in cases of plant height, effective tillers per plant, flag leaf length, flag leaf breadth and grains per panicle. Estimates of all the dominance x dominance (l) type of epistasis were found non-significant. Additive x dominance effect (j) was significant in

only two characters viz., plant height and flag leaf breadth. This indicated that inheritance of these characters is not simple and strait forward. Additive x additive (i) type of gene action in yield/plant was reported by Gill *et al.* (1979) in wheat. Singh and Anand (1971) reported additive x dominance (j) type of interaction in grain number of wheat whereas significant epistasis parameters in some agronomic traits were reported by Bhatt (1972) in wheat and by Hahn and Chae (1987) in rice. Such significant j effects was expected since, the F_1 population mean indicated considerable heterosis in these cases.

The signs of 'h' and 'l' were different in most of the cases suggested the presence of duplicate type of epistasis. The presence of duplicate epistasis was reported by Singh and Anand (1971) and Bhatt (1972) in wheat. The signs of these two estimates were same in case of primary branches per panicle which suggested the presence of complementary type of gene action in this case. Complementary type of gene action involved in the inheritance of culm length of rice was reported by Choi (1990).

The components of variations (D, H, E_1 and E_2) have been estimated by using unweighted least square techniques under inclusive and exclusive analysis as proposed by Mather (1949), Mather and Vines (1952) and Mather and Jinks (1971).

The estimation of components of variation under both inclusive and exclusive analysis showed that the D estimates were significant and greater in magnitude compared to the other

estimates in almost all the characters. Significant estimates of D with greater magnitude suggested that additive component of genetic variations played an important role in the inheritance of these characters. Importance of additivity in the inheritance of quantitative characters have been reported earlier by many investigators such as Yates (1947), Comstock and Robinson (1948) Mather (1949), Jinks (1954) and Hayman (1954 and 1958) in differentent characters of different crops. Walton (1972), Gill *et al.* (1979), Uddin (1983) and many other investigators showed importance of both additive and dominance components of variation, but the former was of more importance in the inheritance of quantitative characters of wheat. In rice too, additive gene actions were reported to be more important in controlling different quantitative characters by Mohamed and Hanna (1965), Chang *et al.*(1965), Wu (1968), Li and Chang (1970), Rahman and Eunus (1973), Sathyanarayaniah and Reddi (1973), Ali *et al.* (1975), Khaleque (1975), Khaleque and Eunus (1975), Singh and Nanda (1976), Shaalai and Aly (1977), Kim and Heu (1977), Yen (1977), Azam (1981), Kumar *et al.* (1986) and Hahn and Chae (1987).

The H estimates during both inclusive and exclusive analysis yielded non-significant negative values. Variance, being a quadratic quantity, can never be negative. Negative estimates of components of variation, however, arose from the sampling errors (Mather, 1949) or due to genotype-environment interaction (Hill,

1966). Such H values are to be considered either as zero or as very small but positive numbers (Mather, 1949). Negative H estimates have been reported by Mather (1949) in Nicotiana, Joarder and Eunus (1968) and Joarder *et al.* (1977) in Rape seed, Paul *et al.* (1978) in Jute and Khaleque *et al.* (1978) in Rice.

Heritability estimates are the potentiality of fixable heritable variability under a particular environment. A great variability was observed in the heritability estimates of different characters. Broad sense heritability (Hb) was high in majority of the characters. The Hb ranged from 41.27% for panicle length to 80.24% for grain yield per plant. High estimates of heritability (Hb) found in the studied characters indicated that the total phenotypic variability in these cases were genetic in nature. The high estimates also indicated that the contribution of additive and/or additive x additive gene effects were more than that of dominance and/or dominance x dominance gene effects. The genetical nature of major part of the phenotypic variation have been reported by Khaleque (1975), Khaleque and Eunus (1975), Chaudhury *et al.* (1976), Shaalai and Aly (1977), Prasad and Chandra (1977), Kumar *et al.* (1986), Alfonso (1988), Tai *et al.* (1989) and Yang and Wang (1990) in grain yield and many other important characters of rice.

Narrow sense heritability (Hn) estimated from the components of variation were variable from characters to characters. The Hn estimates were also found to be very high in all the characters

and these values ranged 98.18% in panicle length to 143.19% in plant height. The high estimates of narrow sense heritability indicated genetic nature of major part of the phenotypic variation in all the cases. Kaul (1972), Kaul and Bhan (1974), Khaleque (1975), Maurya (1976), Kumar *et al.* (1986) and Tai *et al.*(1989) showed that plant height, panicle length, spikelets per panicle, grain number per panicle, grain weight and many other characters were highly heritable.

Parent-offspring regression heritability estimates which were comparable to most of the narrow sense heritabilities were within the limit of expectation. The parent-offspring regression analysis further suggested that most of the phenotypic variations were of genetic in nature.

Degrees of dominance (h_1, h_2 and h_3 related to F_1, F_2 and F_3 generations respectively) for all the nine characters were estimated by potence ratio method. From the result it was revealed that most of the characters showed partial dominance in F_1 and F_2 while over dominance in F_3 generation. The results also indicated that the dominant genes were positive in nature and isodirectionally distributed. It also suggested that longer plant height, panicle length and flag leaf length over shorter plant height, panicle length and flag length; broader flag leaf breadth and larger flag leaf area over narrower flag leaf breadth and smaller flag leaf area respectively; high count of effective tillers per plant, primary branches per panicle and grains per

panicle over low count of effective tillers per plant, primary branches per panicle and grains per panicle and higher grain yield per plant over lower grain yield per plant showed partial dominance. Chang *et al.* (1965), Aquino and Jennings (1966), Heu *et al.* (1968) and Chang and Vergera (1972) found different results for plant height of rice. They found short stature was dominant over long stature of plant height. Both partial and overdominance (either positive or negative) were detected by Azam (1981) for different characters including grain yield in rice. Positive dominancy in different traits of rice is more common and has been reported by many investigators such as Mohamed and Hanna (1965), Wu (1968), Sathyanarayaniah and Reddi (1973), Khaleque and Eunus (1975); Singh and Nanda (1976) and Yen (1977). The discrepancy in the expression of dominance in F_1, F_2 and F_3 generations may be due to change in the distribution of genes in F_2 and F_3 and could result from the repulsion-phase linkages of genes in the partial to overdominance range. Sharma and Ahmad (1980) reported such type of discrepancy in gene expression in days to heading of wheat.

The test of linkage is basically a test of homogeneity of D and H estimates over the statistics of different ranks. Out of the six statistics involving D and H, $V\bar{F}_2$, $V\bar{F}_3$, $W\bar{F}_3/F_2$ and $V\bar{B}_1$ + $V\bar{B}_2$ was of rank 1 and $\bar{V}F_3$ was of rank 2. The item linkage when tested by residual item, it was observed that all the mean square values were non-significant. The non-significant mean square

values indicated absence linkage in all the cases. In presence of linkage, D and H in the $\overline{V}F_3$ will differ from D and H in the first rank statistics and non-allelic gene interaction affects D and H differently over generations as well as over rank of statistics (Hayman and Mather, 1955 and Mather and Jinks, 1971). As the residual item was non-significant in all the characters, which gave non-significant linkage item, it may be assumed that the presence non-allelic gene interaction made no contribution to the second degree of variances and covariances. The non-significant linkage item indicated that the values of D and H did not differed in $V\overline{F}_3$ statistics from those in others, (Mather, 1949 and Mather and Jinks, 1971). On the contrary of this result, Uddin (1983) detected linkage in grain yield and other yield contributing characters of wheat. Azam (1981) also detected linkage in grain yield and some yield contributing characters of rice.

According to Mather (1949) an effective factor is the smallest unit of hereditary material that is capable of being recognized by the methods of biometrical genetics. It may be closely linked gene, or at the lower limit, a single gene. The number of effective factors were calculated by following three methods of estimation as developed by (i) Castle and Wright (1921), (ii) Burton (1951) and (iii) Mather (1949). All the three estimates are based on certain assumptions : (i) all the genes are equally important, (ii) one parent has all the plus genes and

other parent has all the minus genes, (iii) no linkage exists between pertinent genes, (iv) gene effects combine additivity, (v) degree of dominance for all the plus genes is similar and (vi) no interaction exists between pertinent non-allelic genes. Failure of any one of these assumptions listed above to fulfil in the parents will under estimate the number of effective factors. All the three estimates gave more or less similar results in all cases. From results, it was revealed that all the characters studied were controlled by polygenes. The estimates of number of effective factors showed that two to three pairs of gene group were responsible for controlling plant height, panicle length, flag leaf length, flag leaf breadth, flag leaf area and primary branches per panicle while atleast six and eight pairs of gene group were responsible for controlling grain yield per plant and effective tillers per plant respectively. It was found that a large group, at least twenty two pairs, of effective factors were responsible for controlling grains per panicle. Chandraratna and Sakai (1960), Mitra (1962), Mohamed and Hanna (1965), Rajendran and Namboodiri (1971) Rajagopalon *et al.* (1973), Khaleque (1975), Khaleque and Eunus (1977) and Yang and Wang (1990) have reported similar results on polygenic control of various morphological and agronomical characters of rice. On the contrary to this result, single gene pair controlling plant height, culm length, panicle length, primary branches per panicle, spikelet and grain number per panicle and grain yield per plant of rice was reported by

Chaudhury *et al.* (1976), Yen (1977) and Azam (1981).

The present investigation, therefore, indicated that additivity (with greater magnitude), dominance and non-allelic gene interactions are involved in the inheritance of the nine agronomic characters of rice. The role of environment is also presumed. A breeding programme for the improvement of these characters should be designed, that will utilize all these gene effects for effective breeding. It also indicated that a large number of progeny shall have to be raised to get rid of the duplicate types of non-allelic gene interaction because it will hinder progress in selection breeding programme.

SUMMARY

Inheritance of nine quantitative characters viz., plant height, effective tillers per plant, panicle length, flag leaf length, flag leaf breadth, flag leaf area, primary branches per panicle, grains per panicle and grain yield per plant were studied with parents, F_1, F_2, F_3, B_1 and B_2 generations of a single cross of rice (*Oryza sativa* L.) Biometrical techniques were adopted to study the inheritance of quantitative characters.

The means of segregating (F_2, F_3, B_1 and B_2) and non-segregating (F_1) generations were within the parental ranges in all cases. Hybrids did not show better performances than their parents in any of the characters studied. The observed means of all the generations deviated significantly from those of the theoretical arithmatic and geometric means in most of the cases indicating the involvement of non-additive and non-allelic gene effects. Dominance towards better performances of all characters was noticed. Mather's A, B, C and D Scaling Test indicated that non-additive gene actions had affected the means of the segregating generations and also suggested that non-allelic gene actions were involved in the inheritance of these characters.

Epistatic gene action was involved in controlling the mean expression of different generations of the cross. Both additive (d) and non-additive (h) types of gene effects were involved in the inheritance of these characters but the former type was of

much importance than the latter. The estimates of epistatic gene effect (i, j and l) showed that the total epistatic effects varied in different characters and were less than the mean effects (m). Additive x additive (i) type of epistasis was more pronounced than additive x dominance (j) and dominance x dominance (l) types of epistasis. Additive x additive (i) type of of epistasis was found to be significantly operative in five of studied traits viz., plant height, effective tillers per plant, flag leaf length, flag leaf breadth and grains per panicle. In case of plant height and flag leaf breadth additive x dominance (j) type of epistasis was also found to be significantly operative . The epistatic gene effect was found to be duplicate type in all the cases, except primary branches per panicle where it was found to be complementary type.

The estimates of components of variation showed that the additive (D) type of genetic variation of all the characters were greater in magnitude, positive and significant which suggested that additive type of variation formed the major part of the total phenotypic variation in all the cases. It played an important role in the inheritance of these characters. On the other hand, dominance (H) type of genetic variation of all the cases were negative and non-significant. Negative H estimates are to be considered as zero or as very small but positive numbers (Mather, 1949). Thus, the negative H estimates suggested very little contribution of dominance genetic variation in the

inheritance of these characters.

Broad sense heritability (Hb) was high in majority of the cases. It ranged from 41.27% for panicle length to 80.24% for grain yield per plant. Narrow sense heritability (Hn) and heritability estimated by parent offspring regression analysis (P/0) were very high in all the cases. Narrow sense heritability ranged from 98.18% for panicle length to 143.19% for plant height and parent offspring regression ranged from 68.42% for panicle length to 108.33% for plant height.

Dominance relationship as measured by potence ratio method was found to be variable for different generations. The h_1 and h_2 estimates of the degree of dominance suggested partial dominance in F_1 and F_2 generations for most of the characters whereas both partial and overdominance were indicated by the h_3 estimates for different characters of F_3 generation.

The test of linkage was done and no linkage was detected for the characters studied.

The estimates of number of effective factors suggested that all the characters studied were polygenic in nature. Number of effective factors measured by three methods was found to be 2-3 for plant height, panicle length, flag leaf length, flag leaf breadth, flag leaf area and primary branches per panicle, 6-9 for effective tillers per plant and grain yield per plant and 22-26 for grains per panicle. All the three estimates (n_1, n_2 and K_1) gave similar types of information.

PART - II

GENOTYPE - ENVIRONMENT INTERACTION

REVIEW OF LITERATURE

Idea that phenotypic variation comprises genotypic variation due to variation in genetic constitution of varieties and environmental variation caused by environment in which the varieties developed was first formulated by Johannsen in 1909. According to him, genes of an individual are responsible for the development of it but environment has an important role which determines the "Life situation" of the individual. Johannsen (1909), after thorough investigation on dwarf beans (*Phaseolus vulgaris*), concluded that the seed weight of these beans exhibited both heritable and non-heritable variations, whose effects on quantitative characters, like seed weight , were such that only breeding test could distinguish them apart. His work showed the way to a greater understanding of the process of joint regulatory effect of environment and genotype on the development of a particular individual. This understanding was to affect more than just plant breeding.

In 1910, Keeble and Pellow referred to the "well known seasonal variation" which affected the seed weight in peas, adding that caution should be taken whenever data are collected from plant grown in different seasons.

East (1915) reported that the continuous variation of a quantitative character in segregating generation was inherited in Mendelian fashion.

Fisher (1918) developed for the first time a statistical method for partitioning variance of a quantitative character in segregating population into its genetic and environmental components. Hayes (1922), while discussing the production of high-protein quantity in maize, said that there was a very low correlation between protein content of self-fertilized ears of normal varieties and the percentage of protein of their progenies grown in the following year. He suggested that the expression of a character was strongly influenced by environment in which the plant developed and thus, a low correlation could be expected. Parent-offspring correlations were also studied by Immer and Asemus (1931) and Kelly *et al.* (1932). The results they obtained were similar to those obtained by Hayes. All the studies described above focused on the gross effect of environments on life. And these led to further study on the detection and estimation of the interaction between genotypes and environments on the development of individuals. Existence of genotype - environment interaction is indicated by the relative performances of genotypes varying under different environments. Investigation on quantitative characters, the relative performances of different genotypes become more complicated when more than one environment is involved because of the changes in the gene expression which may occur with the changes in the environments. Work in this field goes back to a number of years. Two main approaches have been made for detecting and estimating the

interaction between genotypes and environments. The first one is purely statistical method recognized and proposed by Yates and Cochran (1938). This method is applicable to any number of strains or varieties grown in any number of environments. The method was used by Finlay and Wilkinson (1963) and Eberhart and Russel (1966) to detect and measure the magnitude of genotype-environment interactions in Barley and Maize respectively. They did not try to show any relationship between the components of variance analyses with parameters of biometrical genetics. The second approach involves fitting models which specify the contributions of genetic and environmental actions and genotype-environment interactions to generation means and variances. It also determines the contributions of additive, dominance and non-allelic gene action to the total genetic and interaction components. This approach has been used to estimate genotype-environment interaction in *Nicotiana rustica* by Jinks (1954) and Jinks and Mather (1955).

Following second approach Bucio Alanis (1966) and Bucio Alanis and Hill (1966) studied a pair of inbred lines and the generations that can be derived from an initial cross between them. Their methods of analysis provided more informative conclusions and they can be used to predict across generations as well as across environments. Perkins and Jinks (1968 a and b) bridged over the gap between the two alternative analyses. Expectation of items in the statistical analysis of Yates and

Cochran (1938) was given in terms of models of gene and environmental actions and genotype - environment interaction. The analysis of Bucio Alanis (1966) was extended to cover any number of inbred lines and crosses among them.

Rajas and Sprague (1952) studied the interaction of general and specific combining ability with locations and years for yield in Corn and found that the later interaction were greater than corresponding estimates involving general combining ability. Contrary to the above findings, greater interactions of general combining ability with the environment were observed by Matzinger *et al.* (1959) for yield in Corn; Ling (1967) for yield and other characters in Sorghum and by Paroda and Joshi (1970) for yield and yield components in Wheat.

Widner and Lebsock (1973) studied with ten parent diallel crosses of durum wheat at two locations in North Dakota in 1965 and 1966. An estimate of genotype-environment interaction was determined for grain yield on the means of the F_1, F_2 and parents. Genotype x environment mean squares were significant for the F_1 hybrids and parents but non-significant for the F_2 populations. Bains (1976) studied the G X E interactions in some crosses of spring wheat. The crosses were made on the basis of linear sensitivity of the parental lines to environments. Both the linear and non-linear components of G X E interactions of the advanced generations of each cross were noted. All the aspects of the phenotype including linear and non-linear sensitivity to the

environments were under genetical control.

Islam (1978) made a study with parental and F_1 generations of some wheat crosses under eight different nutritional treatments. He reported that genotype-environment interaction was found to operate in both parental lines and F_1 generations. A significant portion of these interactions was accounted by the linear function of genotype-environment interactions were found under the control of different gene systems. Both additive and dominant gene effects were responsible for the inheritance of the characters he studied.

Chaudhary and Paroda (1979) carried on an experiment with 21 homozygous and heterozygous genotypes of wheat in eight different environments and studied the stability parameters (b and $\bar{S}_d^2$) for grain yield and its components. They reported that the grain yield and its direct components showed the highest response (b) indicating that homozygous populations were buffered less than heterozygous populations.

Jatasra and Paroda (1979) studied ten wheat varieties of Mexican and Indian origin for stability with respect to synchrony traits in six environments. Genotype-environment interactions were found to be a linear component. Three parameters of stability ($\bar{X}$, b and $\bar{S}_d^2$) were positively associated with in case of synchrony of ear emergence and synchrony of height. For these traits synchronous varieties were stable and less responsive to environmental fluctuations.

Singh and Singh (1980) investigated the G X E interactions under seven environments at one location using 22 diverse and the elite cultivars (17 of *T. aestivum* and 5 of *T. durum*). The main effects as well as both the components of G X E interaction (predictable and unpredictable) effects were significant for grain yield. Within hexaploid, the tall cultivars were highly unstable and exhibited low population buffering. Two aspects of phenotype ($\bar{X}$ and b) were positively and significantly associated. However, some of the cultivars exhibited high yield with low and zero regression.

Whingwiri and Kemp (1980) studied the spikelet development and grain yield of wheat ear in response to applied nitrogen. They observed that nitrogen significantly increased tiller number, dry matter and grain yield/plant. Total spikelet numbers increased with increasing nitrogen supply. Nitrogen supply affected grain yield per ear more by influencing the ability of florets to set grain than by varying spikelet number.

Islam *et al.* (1981) investigated variety X seeding date interaction on yield and other agronomic traits of wheat. They showed that the varieties significantly interacted with environment and its interaction was accounted for the linear function of the environmental mean. Genotypes with higher mean performance had regression coefficient greater than the unity compared to the genotypes with low mean performance.

Parh and Khan (1986) worked on G X E interaction of 20 wheat

cultivars at four seeding dates and studied correlation among the stability parameters. They reported that significant positive association was found between the mean performances and regression co-efficient for days to 50% heading and yield/plant. Non-linear component of G X E interaction ($\bar{s}^2_d$) was positive and significantly correlated with days to 50% heading but negatively correlated with days to maturity and plant height. They suggested insignificant correlation in all the parameters for number of tillers per plant, spike length and number by independent genetic mechanism. So, these traits might be expected to attain greater stability and ultimately the yield.

Parh and Khan (1987) studied the G X E interactions on wheat cultivars under four sowing dates. Significant G X E interactions were observed for all the characters. Cultivars suitable for unfavourable environment are Balaka and Baw 28.

Few works on genotype - environment interaction in Rice are available, except the studies on variety x fertilizer interaction in agronomical studies which showed significant variety x fertilizer interaction (Chandraratna, 1961; Kawano and Takahashi, 1968). Summaries of some studies on genotype-environment interaction in Rice are given in the following paragraphs.

Variety x environmental interactions in Rice was studied by Ree *et al.* (1964). He reported that of the interactions between the variety x location and variety x year in Central and Southern Korea, only variety x year interaction in Central Korea was found

to be significant.

Morishima *et al.* (1967) made an analysis of genetic variation in plant type of Rice. They also studied genotype-seasonal variations in different characters by using F_3 lines from the crosses of Peta x 1-geo-tze, which were grown in weight and dry crop seasons. The results of variance analysis showed that genotype x season interaction was significant indicating that the response to the growing seasons was genetically controlled. They concluded that selection for seasonal adaptability and high yielding capacity may be made simultaneously by using certain genetic criteria.

Kawano and Takahashi (1968) studied the inter-relationship among plant characters in Rice and concluded that the genotype x environment interaction was a limiting factor for negative correlations between characters.

Khaleque (1975) worked on genotype-environment interactions for eighteen characters in a 5 x 5 diallel progenies of Rice over two seasons. He mentioned that genotype-environment interactions were operating in both parental and F_2 generations. Both the linear and non-linear components of the genotype-environment interactions were under the control of different gene systems. Both dominant and additive components of variation interact with the environment and were of two different functions of the environment and under the control of different genetic systems.

Khaleque and Eunus (1977) carried out an experiment on

genotype X macro-environment interaction and diversity estimates in rice with 121 varieties over 3 boro seasons during 1970-71, 1971-72 and 1972-73. They observed that the genetic variations were significant for all the characters except yield/plant. They observed high estimates of genetic coefficient of variation (GCV), broadsense heritability (H) and genetic gain (GS) for yield/plant, kernel weight, kernel number, primary branches and flag leaf.

Uddin *et al.* (1979) worked on G X E interaction for two quantitative characters in rice with parental and F_2 generations. They reported that G X E interactions were operative in both parental and F_2 generations. A significant portion of these interaction was accounted for the linear function of the environmental mean. The additive dominance components interacted with the environments and were of different function of the environmental mean. A real difference existed between the populations and there was also a real effect of different doses of nitrogen on these characters. The potence ratio was high in low doses of urea and low in high doses in most of the cases.

Azam (1981) studied genotype-environment interaction for five characters of 12 rice varieties. He found that genotype-environment interactions were operative in all the genotypes and were accounted both for linear and non-linear functions of the environmental means and these were controlled by different gene systems. A real difference between the genotypes existed in

relation to response and stability.

Fifteen rice genotypes of the dry (rainfed) and semidry (rainfed initially with irrigation later) type, were evaluated for stability performance for yield and 4 yield components by Amirthadevarathinam in 1987. He found significant genotype-environment interaction and both linear and non-linear components were equally important. He selected 2 high yielding varieties with wide adaptability and high stability suitable for unfavourable environments.

Alfonso *et al.* (1988) assessed the genotype - environment interaction of 11 genotypes in 4 seasons at 3 localities in 2 years and found greatest varietal differences in performance. He also observed the greatest genotype-environmental interactions occurred during the dry season. He estimated moderate heritability for yield and high heritability for other characters.

Ganesh and Soundrapandian studied the stability parameters in 10 short duration rice varieties under 3 environments in 1988. They found both the linear and non-linear components of genotype-environment interaction contributed to the total genotype-environment interaction and linear component predominated in plant height, number of ear bearing tillers, panicle length, member of filled grains and plot yield. They showed that selections for different environments and high yielding ability can be made simultaneously by using certain genetic criteria.

Narendra *et al.* (1988) studied 25 rice varieties during rainy seasons of 1983 and 1984 and winter of 1983-84 and found significant genotype-environment interaction for days to 50% flowering, plant height and grain yield but not for panicle length of 25 rice varieties. They selected varieties for different environments for winter and rainy seasons and also for poor environments.

However, many investigators have also studied genotype-environment interactions in different crops such as Fripp and Caten (1973) in *Schizophyllum commune*, Zuberi and Gale (1976) in *Papaver dubium*, Joarder and Eunus (1977) in *Brassica campestris*, Uddin *et al.* (1980) in *Oryza sativa*, etc. and they found that the linear relationships existing between the phenotypes and the environments.

The linear relationship usually accounts for most of the variations of genotypes over environments and it is possible to predict phenotypic performances under related environmental conditions. Since a few works have been carried out on genotype - environment interactions in Rice, the present study was undertaken to broaden our knowledge about genotype-environment interactions in relation to yield and some yield component characters of Rice (*Oryza sativa* L.).

MATERIALS AND METHODS

A. MATERIALS

The materials for the present study, G X E interaction, was the same as used in the Part-I study. The materials comprised of non-segregating (Parents and F_1) and segregating (F_2, F_3, B_1 and B_2) generations of the same cross combination (Mut NS3 x Mut NS1) as Part-I study. Some salient features of these two stable mutant lines, used as parents, are as follows :

Mut NS1 : Tall; moderate early maturing, possesses more number of tillers ; leaves are long-broad ; panicles are longer which bear a good number of grains and high yielder type. This mutant line was released under the commercial name "Binasail" by Bangladesh Institute of Nuclear Agriculture in 1987.

Mut NS3 : Semi - dwarf, early maturing, possesses lower number of tillers, leaves are small and moderate broad, panicles are smaller which bear less number of grains and low yielder type.

B. METHODS

The methods used in this study can be described under the following sub-heads :

a) Production of Experimental Seeds,

b) Raising and Maintenance of Experimental Plants,

c) Collection of Data, and

d) Techniques of Analysis.

a) Production of Experimental Seeds

Seeds of parents i.e., two stable mutant lines (Mut NS1 and Mut NS3) were collected from the Plant Breeding Division, Bangladesh Institute of Nuclear Agriculture, Mymensingh, Bangladesh.

Seeds of F_1s, F_2s, F_3s, B_1s and B_2s produced during the years 1988 to 1990 along with seeds of parents were also used in this study.

b) Raising and Maintenance of Experimental Plants

Seedlings of two mutant lines and non-segregating and segregating generations (F_1, F_2, F_3, B_1 and B_2) were raised on homogenous beds which were prepared as small field blocks with urea, triple-super phosphate and muriate of potash as chemical fertilizers for the supply of nitrogen (N), phosphate (P) and potash (K), respectively. Seeds were sown on 7th July, 1991.

Six hundred earthen pots (12" size) were filled up with moderately manured soil (mixed with oil-cake and cow dung). For artificial creation of differences in soil environments N, P and K were used in different combinations. There were altogather eight combinations of N, P and K including zero does i.e, absence of these fertilizers. The eight combinations were zero, N, P, K, NP, NK, PK and NPK. An amount of 7 gm triple-super phosphate and 3 gm muriate of potash were applied to the pots according to

their treatment combinations. Urea was applied in three splits to the respective treatment pots. The three splits 2 gm, 3 gm and 2 gm of urea were applied after 7 days of transplantation, at the maximum tillering stage and at the panicle initiation stage respectively. The experiment was replicated thrice. Transplantation was done on 6ht August, 1991, with 30 days old seedlings. There were altogather 75 pots for $3P_1$, $3P_2$, $3F_1$, $30F_2$ (of $10F_2$ lines), $30F_3$ (10 F_3 lines), $3B_1$, and $3B_2$ plants for each treatment. Thus, considering each combination of fertilizer as an environment there were eight environments for each population in a replication. Usual irrigation and weeding were done whenever necessary.

The experiment was repeated following the same procedure for the second time during 1992. Sowing of seeds was done on 10th July, 1992 and seedlings were transplanted on 9th August, 1992.

During both the years, pots were arranged following randomized block design.

c) Collection of Data

Data were collected on invdividual plant basis. A standard tiller was first selected and then labelled for collecting the data of panicle and flag leaf. The following characters were recorded for the present study :

1. Plant height (PH) (measured in cm.)
2. Effective tillers per plant (ET/P)
3. Panicle length (PL) (measured in cm. from the selected tiller)

4. Flag leaf length (FLL) (measured in cm. from the selected tiller)

5. Flag leaf breadth (FLB) (measured in cm. from the selected tiller).

6. Flag leaf area (FLA) (measured in sq. cm. from the selected tiller

7. Primary branches per panicle (PB/P) (number counted from the selected tiller's panicle)

8. Grains per panicle (G/p) (number counted from the selected tiller's panicle)

9. Grain yield/plant (Gy/p) (measured in gm.)

d) Techniques of Analysis

The biometrical techniques of analysis developed by Fisher (1918), Yates and Cochran (1938), Mather (1949), Mather and Jones (1958), Finlay and Wilkinson (1963), Eberhart and Russel (1966), Bucio Alanis (1966), Bucio Alanis and Hill (1966) and Breese (1969) were followed for the analysis of the collected data.

Means and Analysis of Variance

The means of the seven populations were worked out by taking the arithmetic mean of three replications. The analysis of variance was done by using the data of individual plant of P_1, P_2, F_1, B_1 and B_2 and means of F_2 and F_3 of each replication for testing the significant differences between the populations. Variances of diferent effects were estimated by using the general formula:

$$[\Sigma X^2 - (\Sigma X)^2/n] / [n - 1]$$

Where, X is the individual reading recorded at the time of

collecting data and n is the total number of individual readings in all three replications.

The effect of population i.e., genotype, environment and year and their interactions were determined according to the following formulae:

Item	SS	df
Total	$\Sigma X^2 - (\Sigma X)^2/n$	335
Population(P)	$1/48\ \Sigma P^2 - CF$	6
Environment(E)	$1/42\ \Sigma E^2 - CF$	7
Year (Y)	$1/168\ \Sigma Y^2 - CF$	1
P X E	$(1/6\ \Sigma PXE^2 - CF) - PSS - ESS$	55-6-7 = 42
P X Y	$(1/24\ \Sigma PXY^2 - CF) - PSS - YSS$	13-6-1 = 6
E X Y	$(1/21\ \Sigma EXY^2 - CF) - ESS - YSS$	15-7-1 = 7
P X E X Y	$(1/3\ \Sigma PXEXY^2 - CF) - PSS - ESS - YSS - PXESS - PXYSS - EXYSS$	111-6-7-42 -6-7 = 42
Replication(R)	$1/112\ \Sigma R^2 - CF$	1
Error	$TotalSS - RSS - (1/3\ \Sigma PXEXY^2 - CF)$	335-2-111 = 222

P is the sum of all readings of each population over treatments, years and replications ; Σ is the sum of all readings of each treatment over population, years and replications and Y is the sum of all readings of each year over populations, treatments and replications. Whereas, P SS, E SS and Y SS are the sum of squares of population effects (P), environmental effects (E) and effect of years (Y) respectively. And P X E SS,

E x Y SS, P x Y SS and P x E x Y SS represent the sum of squares of different interactions, R SS represents the sum of squares of replicational effect and CF (Correction factor) is equal to $(\Sigma X)^2/n$.

Mean squares were determined by dividing the individual sum of square (SS) values by their respective degrees of freedom (df) and the mean square values were tested against the error mean square value (Error MS).

Phenotypic Regression, Response and Stability

Finlay and Wilkinson (1963) first gave the formula for determining the phenotypic regression and they represented 'b_i' as the response or coefficient of regression. According to them regression SS and 'b_i' values were determined by the formulae:

$$\text{Regression SS} = (SPXY)^2/SSX$$

and $$\text{Response } (b_i) = SPXY/SSX$$

Where, SPXY was the sum of product of two variables (X and Y) and SSX was the sum of squares of the first variable (X).

The 'b_i' values of Finlay and Wilkinson (1963) correspond to the $1+\beta_i$ values of Eberhart and Russel (1966) and $\beta_i = (b_i-1)$ values of Bucio Alanis (1966), Bucio Alanis and Hill (1966) and Perkins and Jinks (1968a).

Standard error ($\pm Sb_i$) of regression coefficient is estimated according to the formula:

$$\pm Sb_i = [SSY - (SPXY)b_i/(n - 2)/SSX]^{1/2}$$

Where, SSY is the sum of squares of the second variable (Y) and n

is the number of environments.

Stability ($\bar{S}^2_d$) or non-linearity of each genotype was calculated as follows:

= Remainder MS - Error MS

Where, Remainder MS = (SSY - Regression SS)/(n - 2)

Genetical Studies with population Means ($\bar{X}$)

Epistatic Gene Effect :

i) 3-Parameter Model:

The expectation of generation means in terms of segregating and non-segregating generations are as follows :

$$\bar{P}_1 = m + d$$

$$\bar{P}_2 = m - d$$

$$\bar{F}_1 = m + h$$

$$\bar{F}_2 = m + 1/2h$$

$$\bar{F}_3 = m + 1/4h$$

$$\bar{B}_1 = m + 1/2d + 1/2h$$

$$\bar{B}_2 = m - 1/2d + 1/2h$$

Where, m measures the base population mean, d measures the additive gene effects and h measures the dominance gene effects.

An unweighted least square technique developed by Mather (1949) was followed to estimate the parameters. From the estimated parameters the expected means of seven generations were calculated. Then the joint scaling test (χ^2 test) of Cavalli (1952) was done to detect the type of gene action. The degree of freedom of χ^2 test was 7-3 = 4.

The significant chi-square (χ^2) indicates the presence of epistasis which means the additive-dominance model was inadequate due to the presence of non-allelic gene action.

ii) 6-Parameter Model:

When 3-parameter model was not suitable to interprete the gene action due to non-allelic gene interaction, the data were then subjected to Hayman's (1958) 6-parameter model. The expected generation means in terms of 6-parameter model were as follows :

$$\bar{P}_1 = m + d + i$$

$$\bar{P}_2 = m - d + i$$

$$\bar{F}_1 = m + h + l$$

$$\bar{F}_2 = m + 1/2h + 1/4l$$

$$\bar{F}_3 = m + 1/4h + 1/16l$$

$$\bar{B}_1 = m + 1/2d + 1/2h + 1/4i + 1/4j + 1/4l$$

$$\bar{B}_2 = m - 1/2d + 1/2h + 1/4i - 1/4j + 1/4l$$

Where, m measures the base population mean, d measures the additive gene effects, h measures the dominance gene effects, i measures the additive x additive type of non-allelic gene action, j measures the additive x dominance type of non-allelic gene action and l measures the dominance x dominance type of non-allelic gene action.

An unweighted least square technique as described in 3-parameter model was used to estimate these six parameters viz., m, d, h, i, j and l.

Effect of Fertilizers :

Individual phenotypic effects of N, P and K and of their different combinations on each character (calculated from environmental means) were estimated following the formulae as given below :

Effect	N_1	N_1	N_1	N_1	N_0	N_0	N_0	N_0
	P_1	P_1	P_0	P_0	P_1	P_1	P_0	P_0
	K_1	K_0	K_1	K_0	K_1	K_0	K_1	K_0
N =	+	+	+	+	-	-	-	-
P =	+	+	-	-	+	+	-	-
K =	+	-	+	-	+	-	+	-
NP =	+	+	-	-	-	-	+	+
NK =	+	-	+	-	-	+	-	+
PK =	+	-	-	+	+	-	-	+
NPK =	+	-	-	+	-	+	+	-

This means that the effect of N on a genotype/population may be found out by adding the phenotypic means of those cases where N is present minus phenotypic means where N is absent. The effect of NP is devised by summing phenotypic values where both N and P are present or absent minus those values where only one of them is present.

The effects were tested by the variances of effects against the Error MS of the analysis of variance :

$Effect^2/n$ = Variance of effect

RESULTS

A. Means and Analysis of Variance

Population means over three replications, two years and eight nutritional treatments for different segregating and non-segregating generations of all the nine characters were calculated and these are presented in Table-1. Table-2 represents the mean performances of different characters performed by the different populations under eight different environments.

Examination of Table-1 showed that the population means varied within characters and between characters. Different populations showed similar performance for the characters studied. It was found that high mean performances of different characters was resumed by the better parent (P_2). Means of all the characters of the segregating and non-segregating generations (F_1, F_2, F_3, B_1 and B_2) were within the parental ranges as it was expected. These means did not exceeded the better parental means in any of the characters studied. The non-segregating generation F_1 performed better than the segregating generations F_2 and F_3. The means of all the characters of the backcross generations (B_1 and B_2) were also within their respective parental means.

Examination of environmental means (Table-2) indicated that nitrogen treatment, either singly or in combination with others, increased the magnitude of phenotypic means in all characters of all the populations whereas potassium or phosphorus specially

potassium had no or very little effect on the expression of these characters.

Analysis of variance of nine characters viz., plant height (PH), effective tillers per plant (ET/P), panicle length (PL), flag leaf length (FLL), flag leaf breadth (FLB), flag leaf area (FLA), primary branches per plant (PB/P), grains per panicle (G/P) and grain yield per plant (Gy/P) for the seven populations were done separately to test the significant differences of different sources of variation. The results are summarized in Table-3. All the mean squares of main items, population (P) and environment (E), were highly significant against the experimental errors in all the nine cases in all the generations (Table-3). Significant items population (P) and environment (E) indicated that there was a real difference existed between the generations and between the effects of different environments, respectively, in all the cases. The main item year (Y) was also found highly significant in all cases indicating that there was a real difference between the effects of years on all the characters. Among the first order interactions, the mean square values of interaction between the populations and environments (P X E) were either highly significant or significant in all cases showing that high interactions existed between the populations with environments. It suggested that the populations responded differently under different environments for all the characters. In case of interaction of population with years (P X Y), the mean

square values of panicle length (PL), flag leaf length (FLL), flag leaf breadth (FLB), flag leaf area (FLA), grains per panicle (G/P) and grain yield per plant (Gy/P) were also found significant. It indicated that there was a real effect of years on the populations which was different in different populations in respect to these six cases. On the other hand, mean square values of plants height (PH), effective tillers per plant (ET/P) and primary branches per panicle (PB/P) for the interaction of population with year (P X Y) were found non-significant indicating the absence of real effect of years on the populations in these three characters. The non-significant mean square values in all cases for the interaction between environments and years (E X Y) suggested that there was also no interactions between environments and years in any of these cases. Mean square values of second order interaction, populations with environments and years (P X E X Y), were significant in most of the cases except effective tillers per plant (ET/P) and primary branches per panicle (PB/P) indicating that combination of different environments with years had real effects on the populations in these seven traits. While the non-significant mean square values of the other two characters for this interaction indicated that there was no effect of environment and years on the effective tillers per plant (ET/P) and primary branches per panicle (PB/P) of the populations.

B. Phenotypic Regression

i) Joint Regression Analysis :

Since the analysis of variance indicated the presence of significant population x environment interaction (P X E) in all the characters, the data were further analysed following Finlay and Wilkinson (1963).

The eight different combinations of N, P and K were treated as different environments. In order to account for the effects of regression, interaction component of analysis of variance was further partitioned.

During the joint regression analysis the population x environment interaction (P X E) sum of squares, calculated involving all the seven generations, was partitioned into two orthogonal items, one measuring that portion of genotype-environment interactions which was due to differences between the fitted regression lines and the other measuring the accumulated deviations of the observed values around these fitted lines. The deviations of the observed values were the residual item which measured the scattered points around the regression lines. The results of regression analysis are shown in Table-4. It is clear from the results that the major part of the genotype-environment interaction variance was due to difference between the slopes of the linear regressions, i.e., all the populations possessed greater linear relationship with the environments for all the characters and generations concerned. The mean square

items, except the case of primary branches per panicle when tested against their respective experimental errors were found highly significant. It suggested that for these characters the populations had significantly greater portion of linear relationships compared to the experimental errors. The item deviation mean squares of all the cases were very low and found non-significant when tested against their experimental errors suggesting that there were very lower magnitude of deviations from linearity. Variance due to the differences between the slopes of linear regressions were found significantly greater than the deviation mean squares in all the cases. This indicated that in all cases the populations had significantly greater proportion of linear relationships compared to the non-linear relationships with environments. The test of linear regression with the deviation mean square further indicated that the significant linear variations were independent of their respective non-linear variations of genotype - environment interaction. When the item linear regression or heterogeneity alone is significant, the rate of change in genotypic interactions with environments do not vary. Each genotype, therefore, has its own characteristics linear response to the environmental changes. If, on the other hand, the item deviation or residual alone is significant, no relationship exists between the genotypes and the environments. In the present investigation, the item linear regression alone was found to be highly

significant when tested against the experimental errors in all the characters, except primary branches per panicle (PB/P), indicating the presence of only linear type of relationship of all the populations with environments. Thus, the joint regression analysis has transformed a complex tangle of genotype - environment interactions into an orderly series of linearity that can only predict the total genotypic response.

ii) Individual Regression Analysis :

The item P X E in the analysis of variance and the item linear regression in the joint regression analysis were highly significant showing the presence of genotype - environment interactions which were linear in nature. From these two analyses no immediate generalization can be made on the relative performance of each population under changed environments, valid comparison of linearity can only be made by individual regression analysis of each population.

Regression techniques for studying the G X E interactions are among the most widely used methods for investigating the response patterns of genotypes. The performance of each population for every character under different environments was regressed against the corresponding overall environmental means (Yates and Cochran, 1938; Finlay and Wilkinson, 1963; Eberhart and Russel, 1966; Perkins and Jinks, 1968a). Regression of individual values on the eight environmental means for each population were computed. The results of individual regression

analysis are presented in Table-5. The regression coefficients (b_i) of this table correspond to the b_i value of Finlay and Wilkinson (1963) and to the $1+b_i$ value of Eberhart and Russel (1966). After substracting 1 from the b_i value, the β_i value of Perkins and Jinks (1968a) were calculated. For convenience of comparison of regression values, the β_i values are also included in the Table-5. The estimates of non-linearity or stability ($\bar{s}^2_d$) (calculated as Remainder MS - Error MS) and the standard errors ($\pm Sb_i$) of regression coefficients were also included in Table-5. The standard errors of b_i ($\pm Sb_i$) proved to be heterogeneous as the Chi-square (χ^2) values (included in Table-5) indicated that the observed deviations from their expected values were significant in all the cases. Thus, it showed that there were distinct differences between the populations in the amount of deviation around the regression slopes and suggested that these attributes were under genetic control. The actual linear regressions of the seven populations for the nine characters have been graphically represented by the Figures 1 to 9. In order to avoid confusion, individual points were not plotted in the graphs. In fact, regression coefficients measure the response of different genotypes to changing environments. Since these changes are measured by the means of all genotypes, the average range of response for one set of genotype under consideration should have a mean regression coefficient of 1.0. Regression coefficient <1.0 and >1.0 indicated below and above

average response respectively of a genotype for changing environments. Response of different populations for different characters to the changed environments as measured by regression coefficients are discussed below. For plant height (PH), all the populations showed significant responses (Table-5). And these responses showed by all the populations, except P_1 and B_1, were above average response. P_1 and B_1 responded below and near the average response respectively. Stability estimates ($\bar{s}^2_d$) of all the generations were noted to be low and negative in nature indicating that all the generations were stable to the change of environments for the character plant height. All the non-segregating and segregating populations showed significant response for effective tillers per plant (ET/P). Three populations viz., P_2, F_1 and B_2 responded above the average and the other four generations showed either below the average or near the average response (Table-5). However, all the generations showed similar performance for the stability parameter. Stability estimates of the seven generations were found very low (nearer to zero) and negative in nature suggesting all the generations were most stable with changing environments for the character effective tillers per plant. In case of panicle length (PL), all the populations, except P_2 and B_2, exhibited either average responses or below the average response. P_2 and B_2 showed above average response for this character. However, all the b_1 values were found highly significant (Table-5). Similar nature of

stability estimates for this character were found. $\bar{s}^2_d$ values were negative low and nearer to zero indicating that all the non-segregating and segregating generations were stable with the changing environments for panicle length.

With respect to flag leaf length (FLL), regression coefficients (b_1 values) of all the populations were found highly significant (Table-5). P_1 and B_1 showed below the average, F_1, F_2 and F_3 showed near the average and P_2 and B_2 showed the above average response for this trait. Stability values ($\bar{s}^2_d$) were found to be very low and negative in nature showing stable nature of all the generations for this character.

Regression coefficients of all the generations for flag leaf breadth (FLB) were found highly significant (Table-5). The generations P_2, F_1 and B_2 had above average response and F_2, F_3 and B_1 had the response nearer to average. On the other hand P_1 had the below average response. In all the generations stability values for this trait were also found very low and negative indicating stable nature of flag leaf breadth of all the generations. Regression coefficients (b_1 values) of all the generations, except P_1, P_2 and B_2, for the flag leaf area (FLA) were found either equal to or nearer to the unity. P_2 and B_2 exhibited response above the unity while P_1 exhibited response below the unity. All the regression coefficients (b_1) were found highly significant (Table-5). For this character, the estimated stability values of all the populations were low and negative

suggesting stable nature of this trait of all the generations in relation to the change of environments. For the number of primary branches per panicle (PB/P), all the generations responded significantly with the change of environments (Table-5). All the populations, except P_2 and B_2, had average or below average regression coefficients. P_2 and B_2 had above average regression coefficients. Stable nature for this character of all the generations was observed by the low negative stability values.

In case of number of grains per panicle (G/P), regression coefficients of all the generations were highly significant (Table-5). Three generations viz., P_2, F_1 and B_2 showed above average performance while the other four generations showed near average or below average performance. As all the b_1 values were significant, it suggested that number of grains per panicle of all the generations were affected by the change of environments. Estimates of stability ($\bar{S}^2_d$) values indicated that all the populations were stable for this character. For grain yield per plant regression coefficients of P_2, F_1 and B_2 generations were above the average response. On the other hand the response of the other four generations were near the average or below the average response. However, all the regression coefficients were highly significant (Table-5) like the previous characters. This suggested that changed environments had affected grain yield per plant of all the generations. For grain yield per plant,

stability estimates were found very low and negative indicating its stable nature in all the generations.

From regression coefficient values (b_1) of Table-5, it can be summarized that all the b_i values of different characters of different populations were highly significant which indicated that all the nine traits of the non-segregating and segregating generations of the cross were affected by environments. On the other hand, stability values ($\bar{S}_d^2$) of this table were low, negative and did not differed much in a character suggested that all the populations for the studied trials were most stable to different environments and these populations, non-segregating (P_1, P_2 and F_1) and segregating (F_2, F_3, B_1 and B_2) generations showed similar performance in respect of stability parameter.

C. Correlation Studies

Correlation coefficient (r) was calculated by the usual product moment correlation method. Correlation coefficients 'within' as well as 'between' characters were measured and are presented in Table-6 and Table-7, respectively.

i) Correlation within character :

Within characters the correlation coefficients (a) between the population means ($\bar{X}$) and responses (b_1) of the populations, (b) between the population means ($\bar{X}$) and stabilities ($\bar{S}_d^2$) of the populations and (c) between responses (b_1) and stabilities ($\bar{S}_d^2$) of the populations were calculated separately and the results are

shown in Table-6.

a) Correlation between Means ($\bar{X}$) and Responses (b_i) :

All the correlations between the population means ($\bar{X}$) and responses (b_i) of the populations for all the characters studied were found positive and significant (Table-6). It suggested that these two aspects of phenotype were dependent of each other.

b) Correlation between Means ($\bar{X}$) and Stabilities ($\bar{S}^2_d$) :

Mean performances ($\bar{X}$) of the populations were positively associated with stabilities ($\bar{S}^2_d$) in all cases, except plant height and flag leaf breadth where the relationships were negative. In all cases the relationships were non-significant (Table-6). The non-significant association, either positive or negative, indicated that these two aspects of phenotype were independent of each other.

c) Correlation between Responses (b_i) and Stabilities ($\bar{S}^2_d$):

The correlations between responses (b_i) and stabilities ($\bar{S}^2_d$) were non-significant in most of the cases, except panicle length where the relationship was positive (Table-6). The association between these two aspects were negative in three cases viz., plant height, flag leaf length and flag leaf breadth. Non-significant correlations between responses and stabilities in majority cases suggested that these two aspects were also independent of each other and these are controlled by different gene systems.

ii) Correlation between characters :

Correlation co-efficients between means ($\bar{X}$), between responses (b_i) and between stabilities ($\bar{s}^2_d$) among the characters were estimated and are presented in Table-7.

a) Correlation between Means ($\bar{X}$) :

The correlation co-efficients (r) between the means of the population among the characters were positive and significant in all the cases (Table-7) indicating that the means of the studied characters of the populations were directly associated with that of other characters of the populations. In other words, the means of the populations of a character increase or decrease significantly with the increase or decrease of means of other characters of the populations.

b) Correlation between Responses (b_i) :

With respect to correlations between responses among the characters significant correlations were found in all the cases (Table-7) suggesting that the responses of different populations for different characters were directly correlated with that of other characters of the populations i.e., the response of the populations for a character was found to be directly proportional to the change of responses of the populations for other characters.

c) Correlation between Stabilities ($\bar{s}^2_d$) :

In case of stabilities, the correlations of a character with other characters were either positive or negative and most of the

relationships were non-significant. Significant positive association was found in the cases of effective tillers per plant with flag leaf area and panicle length with grain yield per plant and significant negative association was found in case of primary branches per panicle with grains per panicle (Table-7). The non-significant correlations of majority cases suggested that the stabilities of the populations for the characters studied were not in significant association with that of the populations for other characters. The stability of the population for a character may be increased with the increase or decrease of stabilities of other characters but the change was non-significant.

D. Genetical Studies with Means ($\bar{X}$) [Epistatic Gene Effect]

1) 3-Parameter Model :

In absence of epistasis the data fits in 3-parameter model in which m measures the mean effect, d measures the additive effect and h measures the dominance effect. An unweighted least square techniques developed by Mather (1949) was followed to estimate the parameters. The values of m, d and h for different characters thus computed are summarized in Table-8. A χ^2 test was done to test the goodness of fit of the observed generation means with the expected means. The $\chi^2_{df=4}$ obtained for each character is also included in Table-8. The χ^2 values were found significant for plant height and grains per panicle. The χ^2 values of the other seven characters were non-significant. Significant χ^2 values indicated that epistasis was involved in

controlling the means of plant height and grains per panicle of different generations. Results of those traits that had non-significant χ^2 values would be valid under 3-parameter model.

The estimates of mean effect (m) were highly significant in all the characters and were much higher in magnitude than those of additive (d) and dominance (h) effects (Table-8). The additive gene effects (d) were also found significant in all characters studied. However, the additive effects (d) were negative in nature. The dominance effects (h) were found non-significant in all the traits.

The estimates of m, d and h from 3-parameter model will be biased to an unknown extent by effects not attributable to the additive and dominance action of the genes in those cases where χ^2 values were significant.

ii) 6-Parameter Model :

Those two traits, that showed significant χ^2 in 3-parameter model, were then analysed in terms of 6-parameter model following unweighted least square techniques (Mather, 1949) to separate out the epistatic gene effects from m, d and h. The values of m, d, h, i, j, and l estimated in terms of 6-parameter model are presented in Table-9. Here, m measures a mean effect, d and h measure the additive and dominance effects respectively and i, j and l measure the epistatic effects, additive x additive (i), additive x dominance (j) and dominance x dominance (l) types of gene interaction.

The estimates of mean effects (m) and additive effects (d) were significant in both the characters viz., plant height and grains per panicle (Table-9). The magnitude of mean effect (m) was larger than those of additive effects (d) and dominance effects (h) in both the cases. However, the additive effects (d) of both the traits were found significant and negative in nature while on the other hand both the dominance effects (h) were non-significant and positive in nature. The estimates of epistatic effects (i, j and l) showed that the magnitude of all the epistatic effects in both the traits were less than the mean effects (m). The additive x additive (i) epistasis in both the cases were non-significant but the epistasis i in plant height was found negative and in grains per panicle it was positive in nature. Additive x dominance (j) type of epistasis was found positive while dominance x dominance (l) type of epistasis was found negative in nature in both the characters studied. However, additive x dominance (j) type of epistasis in plant height was found significant and greater in magnitude than the other types of epistasis. Opposite signs of 'h' and 'l' were observed in both the traits indicating the presence of duplicate type of gene action in these cases.

E. Effects of Fertilizers

In the analysis of variance all the mean square values of the item environment (E) for all the characters were significant against the experimental errors (Table-3) indicating that the

used fertilizers had significant effects on different characters of the populations. However, on the relative effects of different fertilizers on different characters of the populations no comparison can be made unless the individual environmental effects on the characters are separated. The significant mean square values of the item environment (E) of analysis of variance was, therefore, partitioned corresponding to the different fertilizer combinations on the different characters of different populations.

Firstly, the effect of different fertilizers individually and in combination with others were calculated from the overall environmental means. All the fertilizers, (viz., N, P and K) singly showed positive effects on all the characters and these effects, except the case of potash (K) on flag leaf length (FLL), were found significant (Table-10). The effects of fertilizers when combined with others were either positive or negative as well as non-significant in nature except the case of urea in combination with phosphate (NP) on four characters of the populations. Urea with phosphate (NP) had significant positive effects on effective tillers per plant (ET/P), primary branches per panicle (PB/P), grains per panicle (G/P) and grain yield per plant (Gy/P).

Individual effects as well as the effects of different combinations of N, P and K on different characters of different populations were separately calculated from the means over

replications and years. The results are summarized in Table-11. Application N, P and K singly had highly significant positive effects on plant height of all the seven populations (Table-11). On the other hand, different combinations of N, P and K though had positive effects on plant height of all the populations, the effects were non-significant.

In case of effective tillers per plant, all the individual effects or the effects of different combinations of N, P and K on all the populations were positive in nature. However, N, P and K individually had highly significant effects on effective tillers per plant of all the populations (Table-11). Among the different combinations, NP in P_1 and PK and NPK in F_1 also had significant effects on this character.

Individual effects of N, P and K application on panicle length of different populations were found positive and highly significant. On the other hand, different combinations of N, P and K showed both positive and negative effects, which were non-significant, on panicle length of the seven populations.

Flag leaf length of all the populations were affected positively by N, P and K when applied singly or by the different combinations of these fertilizers. However, only N and P showed highly significant effects on flag leaf length of all the populations. Significant effects of K on this trait were also observed in P_1, F_1, and F_3 populations (Table-11).

Highly significant positive effects of N, P and K, when

applied singly, were observed in case of flag leaf breadth of all the populations (Table-11). Non-significant positive effects by PK and NPK were found while NP showed non-significant negative effects for flag leaf breadth in all the populations. NK showed both positive and negative non-significant effects for this character of all the seven populations.

In case of flag leaf area, all the individual effects of N, P and K were positive and highly significant in all the populations. The effects of different combinations of N, P and K on flag leaf area of all the populations were also positive but non-significant, except the effects of PK and NPK in F_1 which were significant.

All the individual effects or the effects of different combinations of N, P and K on primary branches per panicle were positive in all the populations. The individual effects of these fertilizers or the combinations NP and NK were significant, except the case of NK in P_2 (Table-11). Significant effects of PK in F_3 and B_2 and of NPK in F_1 were also observed.

In case of grains per panicle, all the individual effects and the effects of different combinations of N, P and K on all the populations were positive and significant, except some effects of NK, PK and NPK (Table-11). The effects of NK and PK application on grains per panicle of P_1 and backcross generations were found non-significant. Application of NPK also showed non-significant effects on this trait of P_1, F_3 and backcross generations.

All the individual effects of N, P and K, except K in P_1 and the combination NP, except in P_1, showed highly significant positive effects on grain yield per plant of all the populations (Table-11). NK showed non-significant positive effects while PK, except in P_2, showed non-significant negative effects. The effect of PK in P_2 was found highly significant and positive. The only significant effect of NPK, which showed positive nature, was found in P_2 for this trait.

Table-1

Mean performances of different characters of different populations.

Populations	PH	ET/P	PL	FLL	FLB
$\bar{P}_1$	74.1	5.9	21.5	26.4	1.19
$\bar{P}_2$	113.8	7.7	23.9	32.8	1.41
$\bar{F}_1$	106.4	7.0	23.2	30.5	1.34
$\bar{F}_2$	104.1	6.6	22.5	30.2	1.31
$\bar{F}_3$	105.6	6.6	22.9	30.1	1.30
$\bar{B}_1$	99.8	6.6	22.5	30.4	1.30
$\bar{B}_2$	110.0	7.4	23.6	31.8	1.37

Continued overleaf

Table-1(Continued)

Mean performances of different characters of different populations.

Populations	FLA	PB/P	G/P	Gy/P
$\bar{P}_1$	21.4	8.0	70.1	6.4
$\bar{P}_2$	31.9	10.2	186.0	20.0
$\bar{F}_1$	28.0	9.5	144.7	15.7
$\bar{F}_2$	27.1	9.4	136.7	13.3
$\bar{F}_3$	26.8	9.4	137.9	13.8
$\bar{B}_1$	26.6	8.8	137.7	11.9
$\bar{B}_2$	28.1	9.9	167.4	17.6

PH = Plant height
ET/P = Effective tillers/plant
PL = Panicle length
FLL = Flag leaf length
FLB = Flag leaf breadth
FLA = Flag leaf area
PB/P = Primary branches/panicle
G/P = Grains/panicle
Gy/P = Grain yield/plant

Table-2

Environmental means of different characters performed by different populations under different environments.

Environments	PH	ET/P	PL	FLL	FLB
Zero	81.3	4.9	18.3	24.2	1.09
N	111.3	7.9	25.0	32.8	1.42
P	87.6	5.2	19.6	26.2	1.19
K	85.2	5.2	19.0	25.4	1.16
NP	118.6	8.6	26.9	35.2	1.45
NK	115.1	8.0	25.9	34.2	1.44
PK	91.6	5.5	20.4	27.2	1.24
NPK	125.2	9.4	28.0	37.2	1.54

Continued overleaf

Table-2 (Continued)

Environmental means of different characters performed by different populations under different environments.

Environments	FLA	PB/P	G/P	Gy/P
Zero	17.6	7.1	86.9	5.7
N	31.0	10.1	171.8	19.6
P	21.0	7.9	97.0	6.9
K	19.6	7.3	93.0	6.4
NP	34.0	11.2	188.7	22.5
NK	32.8	10.4	177.9	20.6
PK	22.8	8.2	103.1	7.3
NPK	38.3	12.4	202.1	23.7

PH = Plant height
ET/P = Effective tillers/plant
PL = Panicle length
FLL = Flag leaf length
FLB = Flag leaf breadth
FLA = Flag leaf area
PB/P = Primary branches/panicle
G/P = Grains/panicle
Gy/P = Grain yield/plant

Table-3

Results of analysis of variance with combined years (only mean square values of differnent characters are given).

Item	DF	PH	ET/P	PL
Total	335	421.30***	3.50***	16.29***
Population (P)	6	8150.68***	16.51***	29.22***
Environment (E)	7	12523.44***	136.81***	624.80***
Year (Y)	1	299.83***	39.36***	327.00***
P X E	42	31.05***	0.36*	2.95***
P X Y	6	18.35	0.29	4.89***
E X Y	7	1.47	0.18	1.92
P X E X Y	42	14.28*	0.07	2.14*
Replication	2	28.92	0.70	2.30
Error	222	9.84	0.24	1.44

Continued overleaf

Table-3 (Continued)

Results of analysis of variance with combined years (only mean square values of differnent characters are given).

Item	DF	FLL	FLB	FLA
Total	335	31.19***	0.034***	71.94***
Population (P)	6	191.21***	0.234***	457.98***
Environment (E)	7	952.21***	1.138***	2438.47***
Year (Y)	1	230.01***	0.252***	576.51***
P X E	42	13.33***	0.009***	16.46**
P X Y	6	14.11*	0.018***	21.85*
E X Y	7	0.45	0.004	8.60
P X E X Y	42	8.89*	0.006*	14.93*
Replication	2	1.67	0.004	3.15
Error	222	6.21	0.004	9.87

Continued overleaf

Table-3 (continued)

Results of analysis of variance with combined years (only mean square values of differnent characters are given).

Item	DF	PB/P	G/P	Gy/P
Total	335	4.04***	3429.31***	81.04***
Population (P)	6	24.39***	62388.11***	908.56***
Environment (E)	7	161.44***	101270.50***	2760.95***
Year (Y)	1	27.77***	11597.25***	131.25***
P X E	42	0.24*	950.92***	37.72***
P X Y	6	0.15	164.35***	2.99
E X Y	7	0.17	52.00	2.79
P X E X Y	42	0.03	63.01*	3.07*
Replication	2	0.22	130.81	4.63
Error	222	0.16	44.15	2.16

*, ** and *** Indicate significant at 5%, 1% and 0.1% level, respectively.

PH = Plant height
ET/P = Effective tillers/plant
PL = Panicle length
FLL = Flag leaf length
FLB = Flag leaf breadth
FLA = Flag leaf area
PB/P = Primary branches/panicle
G/P = Grains/panicle
Gy/P = Grain yield/plant

Table-4

Joint regression analysis for linearity and non-linearity.

Item	SS	DF	MS	VR_1	VR_2
Plant height :					
Total	69299.74	167	414.97	74.10***	
Population (P)	24253.92	6	4042.32	721.84***	
Environment(E)	43780.00	7	6254.29	1116.84***	
P X E	638.60	42	15.20	2.71***	
Heterogeneity of					
Regression	400.17	6	66.70	11.91***	3970.00***
Deviation	0.69	36	0.04	0.003	
Error (with replicate)	627.22	112	5.60		
Effective tillers/plant :					
Total	540.78	167	3.24	108.00***	
Population (P)	50.11	6	8.35	278.33***	
Environment(E)	479.40	7	68.49	2283.00***	
P X E	7.76	42	0.18	6.00***	
Heterogeneity of					
Regression	1.38	6	0.23	7.67***	109.57***
Deviation	0.06	36	0.002	0.07	
Error (with replicate)	3.51	112	0.03		

Continued overleaf

Table-4 (Continued)

Joint regression analysis for linearity and non-linearity.

Item	SS	DF	MS	VR_1	VR_2
Panicle length :					
Total	2401.03	167	14.38	29.96***	
Population (P)	87.35	6	14.56	30.33***	
Environment(E)	2197.80	7	313.97	654.10***	
P X E	62.07	42	1.48	3.08***	
Heterogeneity of					
Regression	38.09	6	6.35	13.23***	441.00***
Deviation	0.52	36	0.014	0.03	
Error (with replicate)	53.81	112	0.48		
Flag leaf length :					
Total	4465.16	167	26.74	13.93***	
Population (P)	583.19	6	97.20	50.63***	
Environment(E)	3382.73	7	483.25	251.69***	
P X E	283.91	42	6.76	3.52***	
Heterogeneity of					
Regression	141.14	6	23.52	12.25***	3062.50***
Deviation	0.29	36	0.00	0.004	
Error (with replicate)	215.33	112	1.92		

Continued overleaf

Table-4 (Continued)

Joint regression analysis for linearity and non-linearity.

Item	SS	DF	MS	VR_1	VR_2
Flag leaf breadth :					
Total	4.953	167	0.0299	33.00***	
Population (P)	0.680	6	0.1133	125.89***	
Environment(E)	3.984	7	0.5691	632.33***	
P X E	0.184	42	0.0044	4.89***	
Heterogeneity of					
Regression	0.012	6	0.0020	2.22*	20.18***
Deviation	0.003	36	0.0001	0.11	
Error (with replicate)	0.105	112	0.0009		
Flag leaf area :					
Total	9811.85	167	58.75	32.46***	
Population (P)	1315.49	6	219.25	121.13***	
Environment(E)	8171.70	7	1167.39	644.97***	
P X E	121.83	42	2.90	1.60*	
Heterogeneity of					
Regression	35.09	6	5.85	3.23***	40.37***
Deviation	5.21	36	0.14	0.08	
Error (with replicate)	202.83	112	1.81		

Continued overleaf

Table-4 (Continued)

Joint regression analysis for linearity and non-linearity.

Item	SS	DF	MS	VR_1	VR_2
Primary branches/panicle :					
Total	644.02	167	3.86	55.14***	
Population (P)	69.85	6	11.64	166.29***	
Environment(E)	560.87	7	80.12	1144.57***	
P X E	4.96	42	0.12	1.71*	
Heterogeneity of					
Regression	0.84	6	0.14	2.00	33.33***
Deviation	0.14	36	0.004	0.06	
Error (with replicate)	8.34	112	0.07		
Grains/panicles :					
Total	562607.81	167	3368.91	1011.68***	
Population (P)	187170.55	6	31195.09	9367.89***	
Environment(E)	355094.12	7	50727.73	15233.55***	
P X E	19970.73	42	475.49	142.79***	
Heterogeneity of					
Regression	6603.60	6	1100.61	330.51***	786.93***
Deviation	50.09	36	1.39	0.42	
Error (with replicate)	372.41	112	3.33		

Continued overleaf

Table-4 (Continued)

Joint regression analysis for linearity and non-linearity.

Item	SS	DF	MS	VR_1	VR_2
Grain yield/plant :					
Total	13249.96	167	79.34	330.58***	
Population (P)	2715.92	6	452.65	1886.04***	
Environment(E)	9710.87	7	1387.27	5780.29***	
P X E	795.65	42	18.94	78.92***	
Heterogeneity of					
Regression	253.54	6	42.26	176.08***	2201.00***
Deviation	0.74	36	0.02	0.08	
Error (with replicate)	27.32	112	0.24		

* and *** Indicate significant at 5% and 0.1% level, respectively.

Table-5

Regression coefficient (b_i and β_i), standard error of b_i ($\pm Sb_i$) and stability (S^2_d) of different characters of different populations.

	Population	b_i	$\beta_i = b_i - 1$	$\pm Sb_i$	S^2_d
Plant height:	P_1	0.72***	-0.28	0.0045	-4.95
	P_2	1.11***	0.11	0.0025	-4.96
	F_1	1.04***	0.04	0.0023	-4.97
	F_2	1.03***	0.03	0.0030	-4.97
	F_3	1.04***	0.04	0.0012	-4.98
	B_1	0.98***	-0.02	0.0018	-4.98
	B_2	1.09***	0.09	0.0018	-4.98
Bartlett's Homogeneity Test : $\chi^2_{(df=6)} = 15.12^*$					
Effective tillers/plant:	P_1	0.89***	-0.11	0.0041	-0.0554
	P_2	1.13***	0.13	0.0028	-0.0552
	F_1	1.05***	0.05	0.0128	-0.0521
	F_2	0.96***	-0.04	0.0092	-0.0540
	F_3	0.95***	-0.05	0.0100	-0.0548
	B_1	0.96***	-0.04	0.0048	-0.0555
	B_2	1.08***	0.08	0.0076	-0.0547
Bartlett's Homogeneity Test : $\chi^2_{(df=6)} = 13.42^*$					

Continued overleaf

Table-5 (Continued)

Regression coefficient (b_i and β_i), standard error of b_i ($\pm Sb_i$) and stability ($\bar{S}^2_d$) of different characters of different populations.

	Population	b_i	$\beta_i = b_i - 1$	$\pm Sb_i$	$\bar{S}^2_d$
Panicle length:	P_1	0.92***	-0.08	0.0092	-0.4084
	P_2	1.09***	0.09	0.0190	-0.3776
	F_1	1.00***	0	0.0101	-0.4063
	F_2	0.98***	-0.02	0.0023	-0.4164
	F_3	1.00***	0	0.0062	-0.4128
	B_1	0.97***	-0.03	0.0069	-0.4118
	B_2	1.03***	0.03	0.0125	-0.3998
Bartlett's Homogeneity Test : $\chi^2_{(df=6)}$ = 27.63***					
Flag leaf length:	P_1	0.88***	-0.12	0.0070	-0.7292
	P_2	1.10***	0.10	0.0061	-0.7313
	F_1	1.02***	0.02	0.0024	-0.7369
	F_2	1.01***	0.01	0.0026	-0.7367
	F_3	0.99***	-0.01	0.0051	-0.7332
	B_1	0.95***	-0.05	0.0079	-0.7269
	B_2	1.06***	0.06	0.0085	-0.7250
Bartlett's Homogeneity Test : $\chi^2_{(df=6)}$ = 17.11**					

Continued overleaf

Table-5 (Continued)

Regression coefficient (b_i and β_i), standard error of b_i ($\pm Sb_i$) and stability (S^2_d) of different characters of different populations.

	Population	b_i	$\beta_i = b_i - 1$	$\pm Sb_i$	S^2_d
Flag leaf breadth:	P_1	0.87***	-0.13	0.0252	-0.0009
	P_2	1.12***	0.12	0.0114	-0.0010
	F_1	1.05***	0.05	0.0260	-0.0009
	F_2	0.99***	-0.01	0.0084	-0.0010
	F_3	0.97***	-0.03	0.0144	-0.0010
	B_1	0.98***	-0.02	0.0120	-0.0010
	B_2	1.06***	0.06	0.0135	-0.0010
Bartlett's Homogeneity Test : $\chi^2_{df=6)} = 14.97^*$					
Flag leaf area:	P_1	0.79***	-0.21	0.0089	-1.81
	P_2	1.19***	0.19	0.0163	-1.73
	F_1	1.00***	0	0.0347	-1.33
	F_2	0.99***	-0.01	0.0177	-1.71
	F_3	1.00***	0	0.0035	-1.84
	B_1	0.99***	-0.01	0.0099	-1.80
	B_2	1.03***	0.03	0.0095	-1.80
Bartlett's Homogeneity Test : $\chi^2_{(df=6)} = 37.89^{***}$					

Continued overleaf

Table-5 (Continued)

Regression coefficient (b_i and β_i), standard error of b_i ($\pm Sb_i$) and stability ($\bar{S}^2_d$) of different characters of different populations.

	Population	b_i	$\beta_i = b_i - 1$	$\pm Sb_i$	$\bar{S}^2_d$
Primary branches/panicle:	P_1	0.87***	-0.13	0.0180	-0.0701
	P_2	1.08***	0.08	0.0104	-0.0710
	F_1	1.02***	0.02	0.0128	-0.0696
	F_2	0.99***	-0.01	0.0086	-0.0720
	F_3	1.00***	0	0.0156	-0.0674
	B_1	0.95***	-0.05	0.0055	-0.0732
	B_2	1.07***	0.07	0.0196	-0.0715
Bartlett's Homogeneity Test : $\chi^2_{(df=6)} = 13.97^*$					
Grains/panicle:	P_1	0.51***	-0.49	0.0063	-2.45
	P_2	1.32***	0.32	0.0096	-1.57
	F_1	0.97***	0.03	0.0072	-2.23
	F_2	0.97***	-0.03	0.0093	-1.64
	F_3	0.99***	-0.01	0.0015	-3.08
	B_1	0.99***	-0.01	0.0100	-1.43
	B_2	1.20***	0.20	0.0110	-1.08
Bartlett's Homogeneity Test : $\chi^2_{(df=6)} = 20.75^{**}$					

(Continued overleaf)

Table-5 (Continued)

Regression coefficient (b_i and β_i), standard error of b_i ($\pm Sb_i$) and stability ($\bar{S}^2_d$) of different characters of different populations.

	Population	b_i	$\beta_i = b_i - 1$	$\pm Sb_i$	$\bar{S}^2_d$
Grain yield/	P_1	0.46***	-0.54	0.0074	-0.1867
plant:	P_2	1.40***	0.40	0.0106	-0.1601
	F_1	1.11***	0.11	0.0060	-0.1955
	F_2	0.94***	-0.06	0.0028	-0.2085
	F_3	0.98***	-0.02	0.0030	-0.2079
	B_1	0.84***	-0.16	0.0036	-0.2060
	B_2	1.26***	0.26	0.0057	-0.1972

Bartlett's Homogeneity Test : $\chi^2_{(df=6)} = 19.88^{**}$

*, ** and *** Indicate significant at 5%, 1% and 0.1% level, respectively.

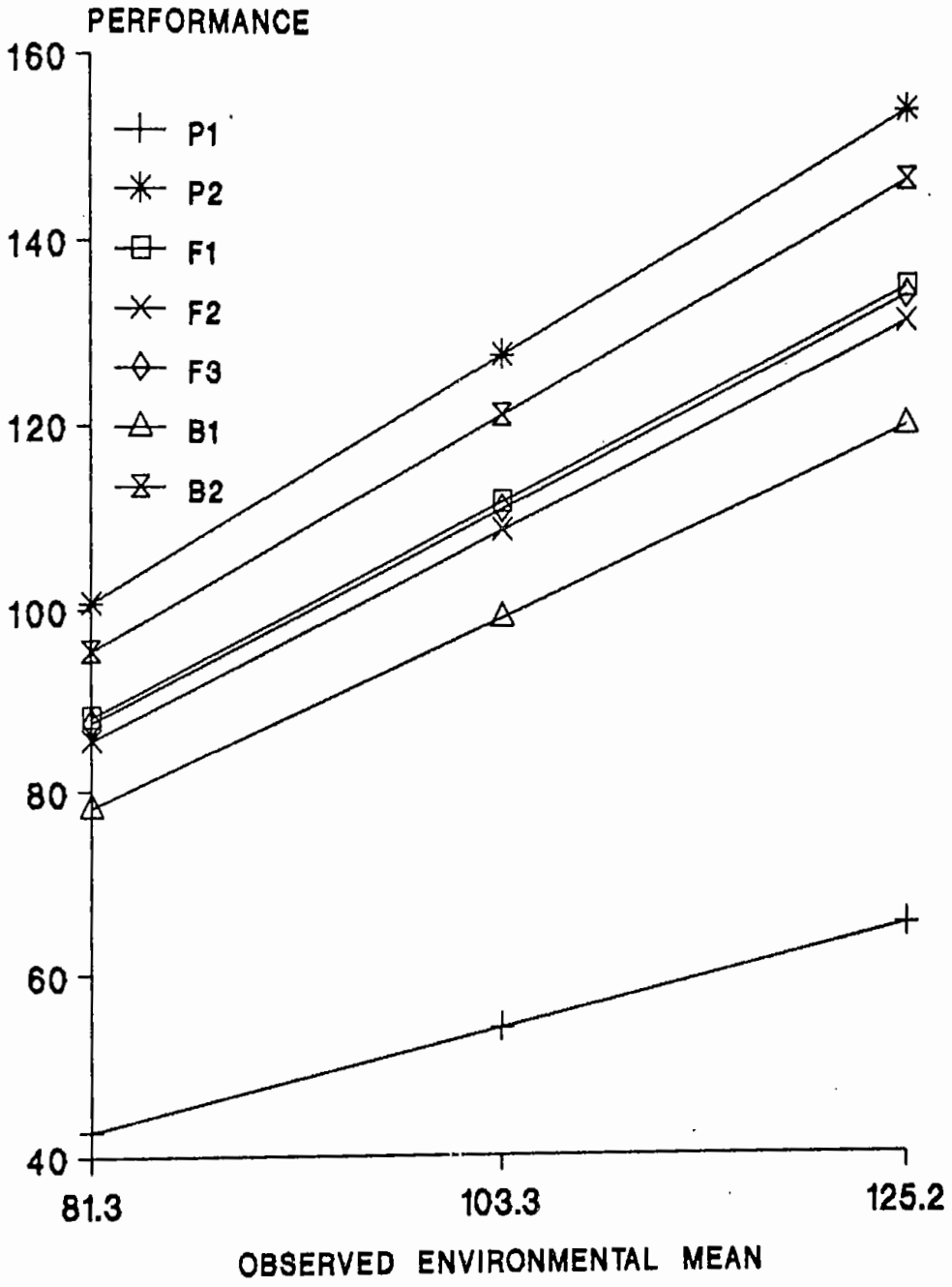

Fig. 1. Regression of different populations on means of plant height under eight different environments.

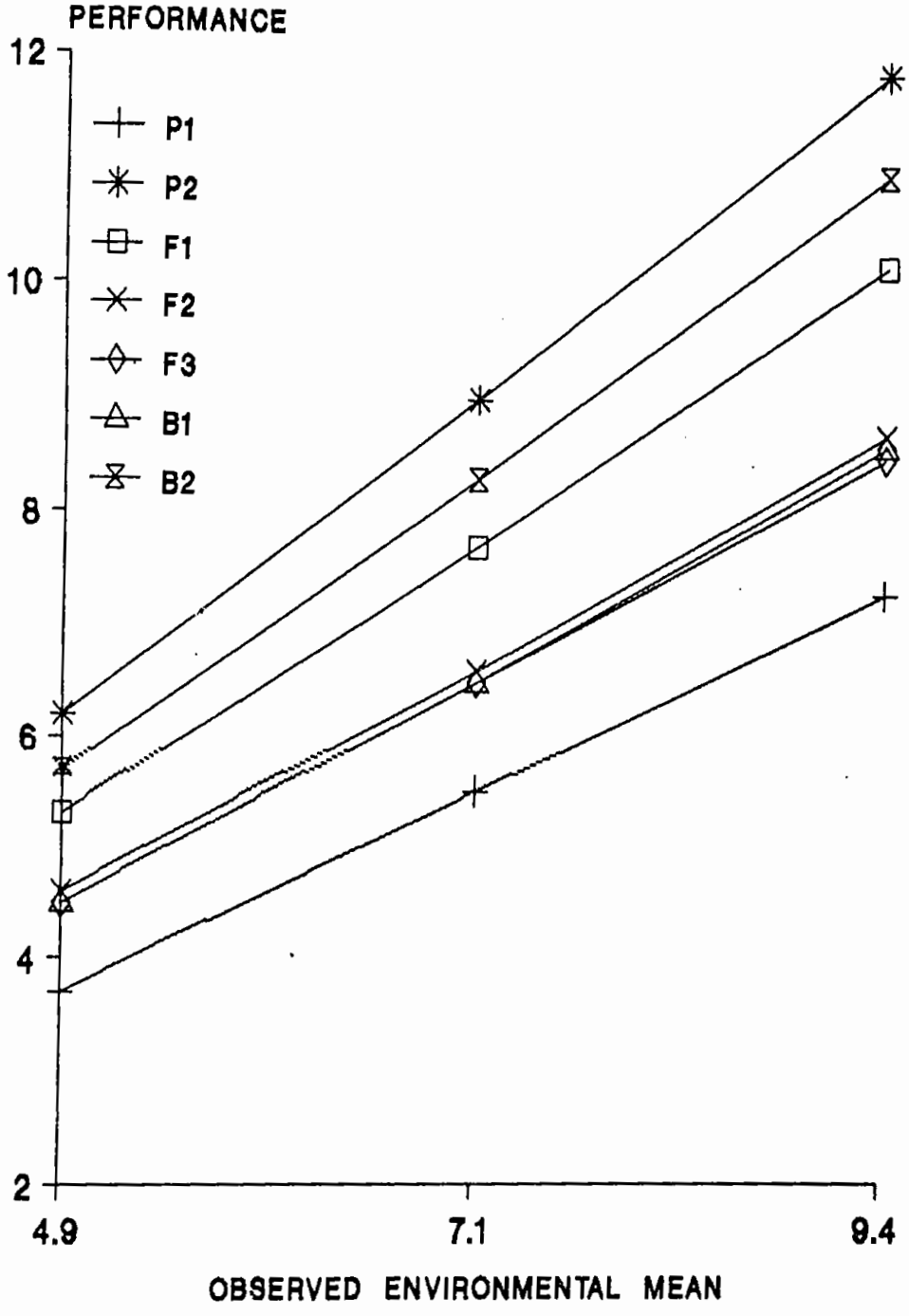

Fig. 2. Regression of different populations on means of effective tillers per plant under eight different environments.

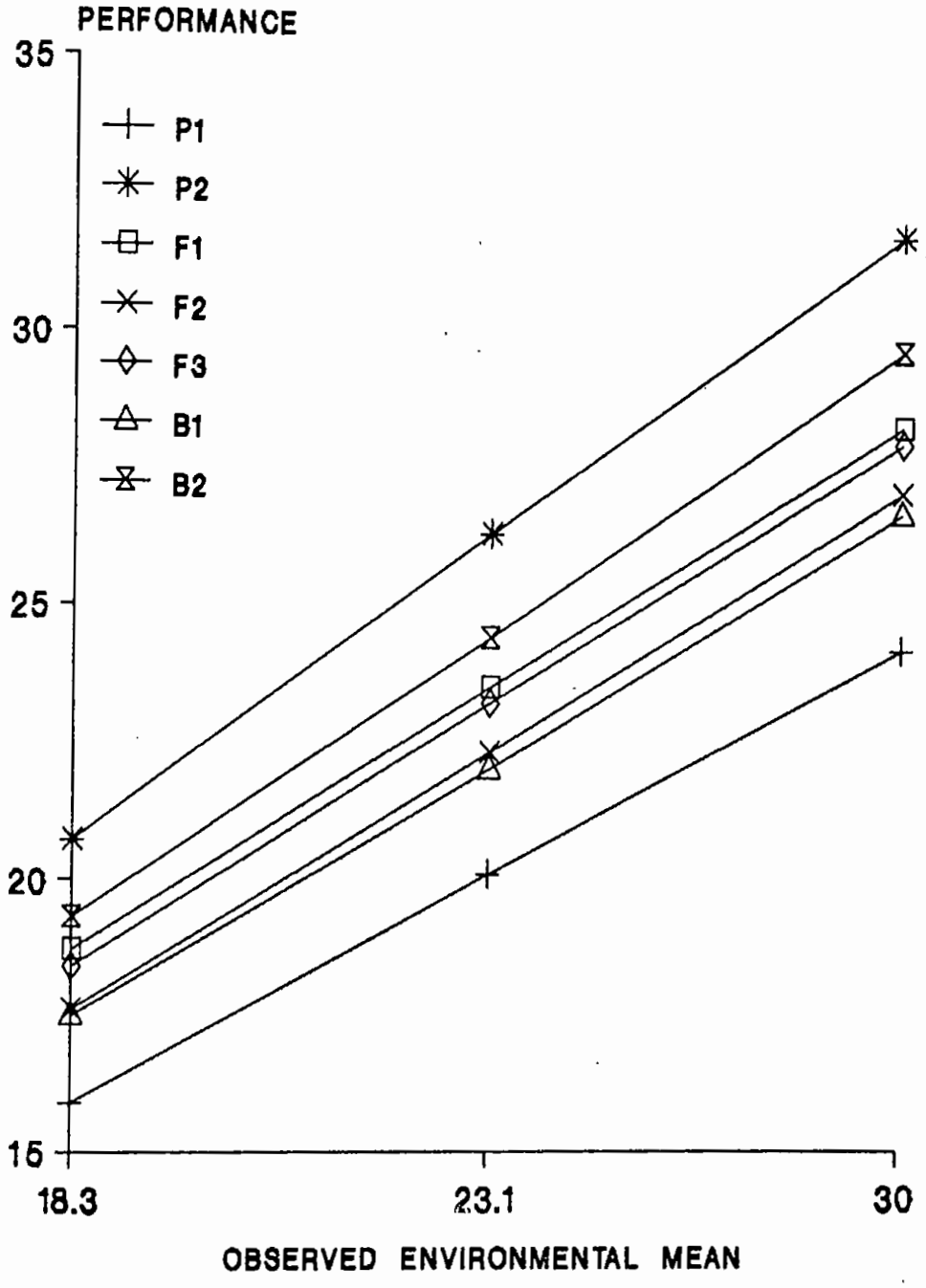

Fig. 3. Regression of different populations on means of panicle length under eight different environments.

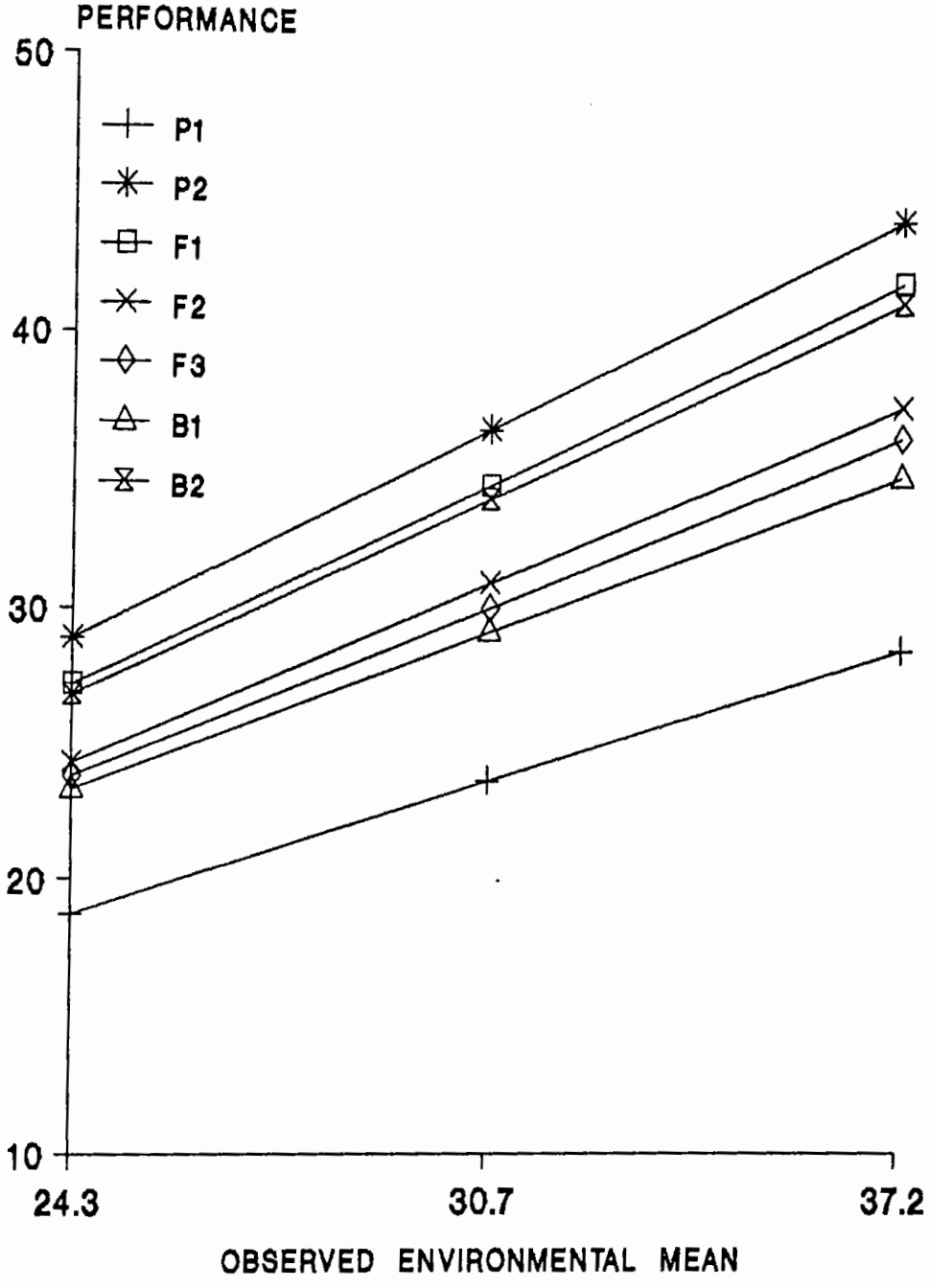

Fig. 4. Regression of different populations on means of flag leaf lenght under eight different environments.

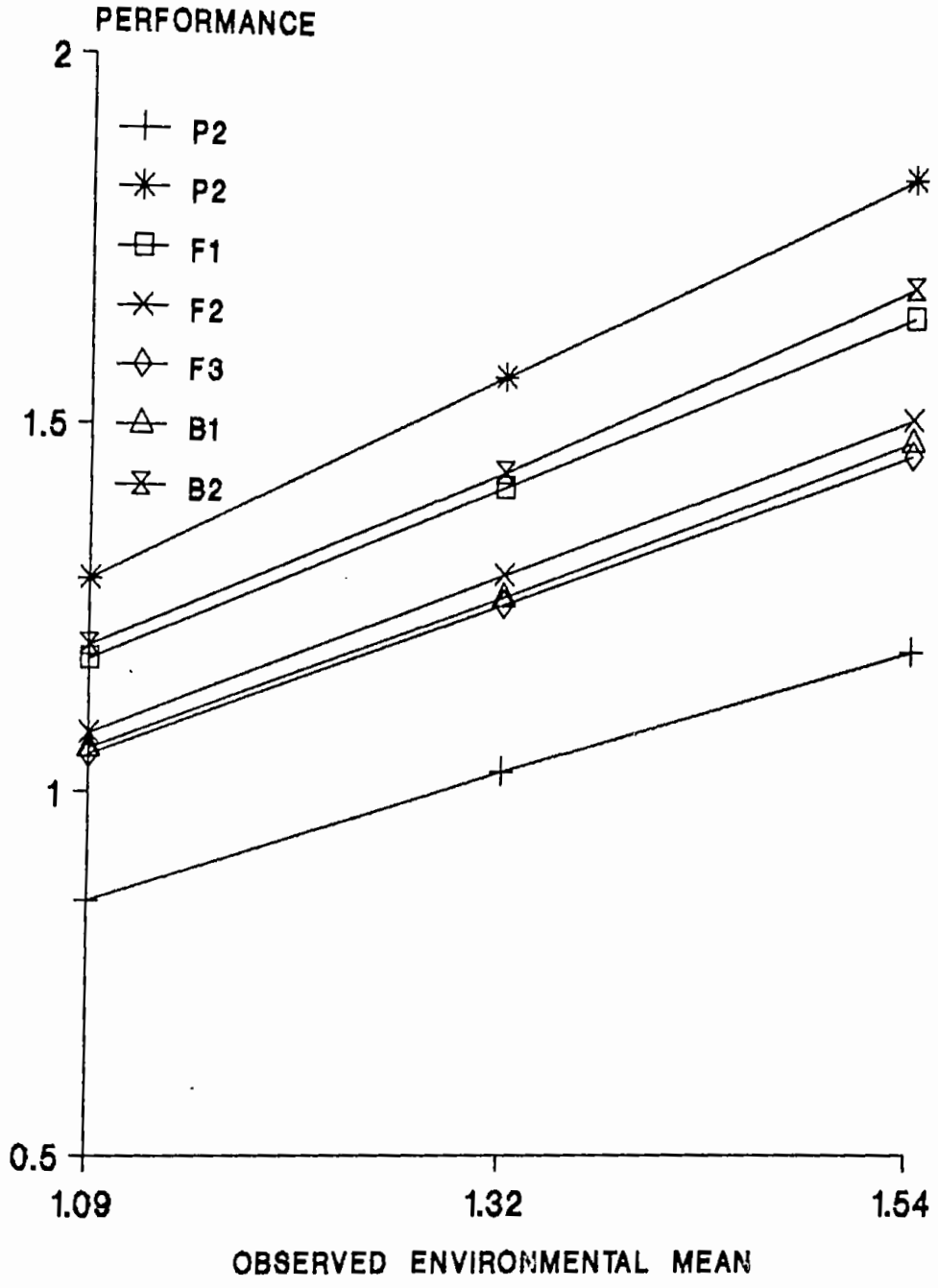

Fig. 6. Regression of different populations on means of flag leaf breadth under eight different environments.

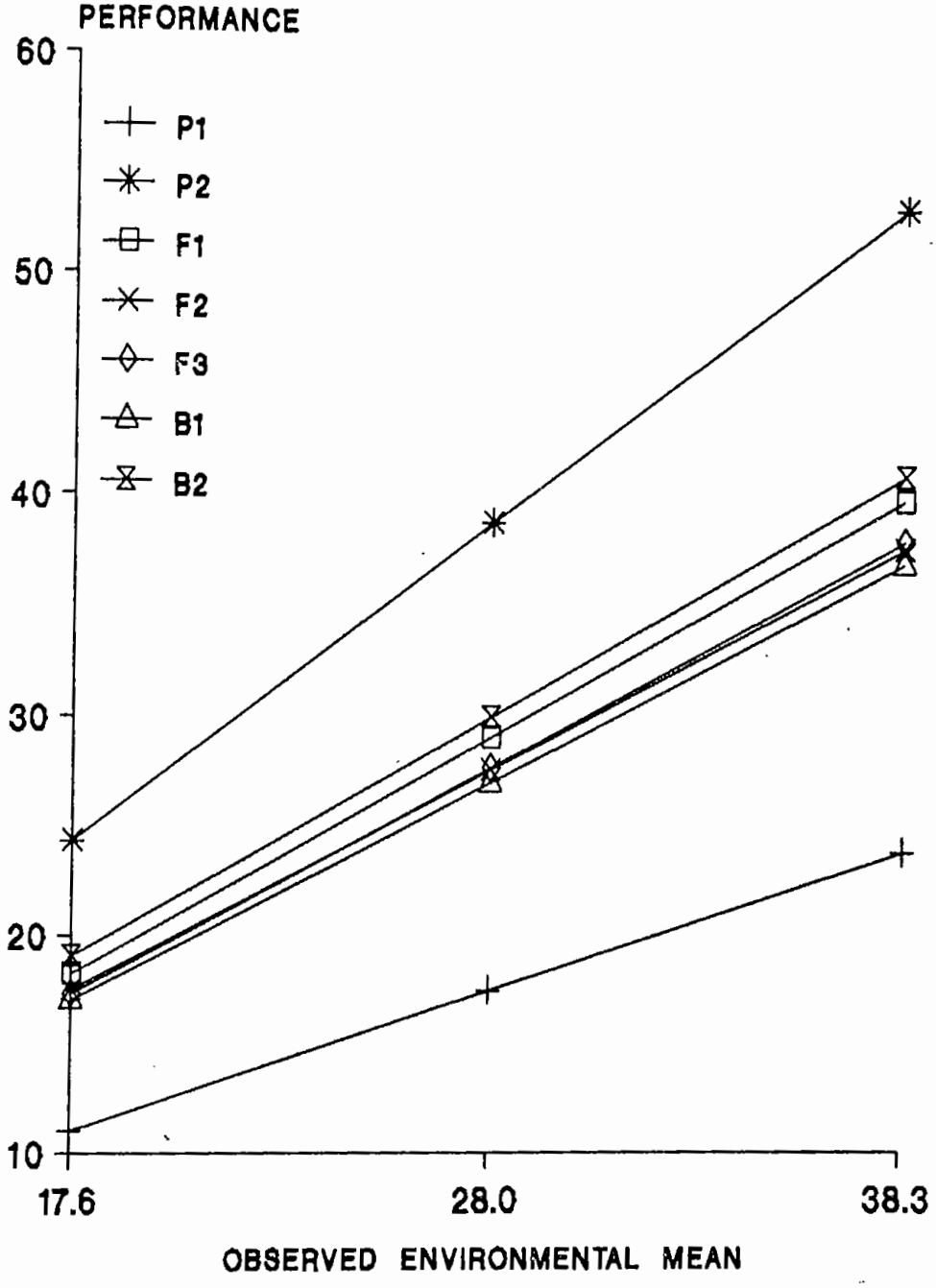

Fig. 6. Regression of different populations on means of flag leaf area under eight different environments.

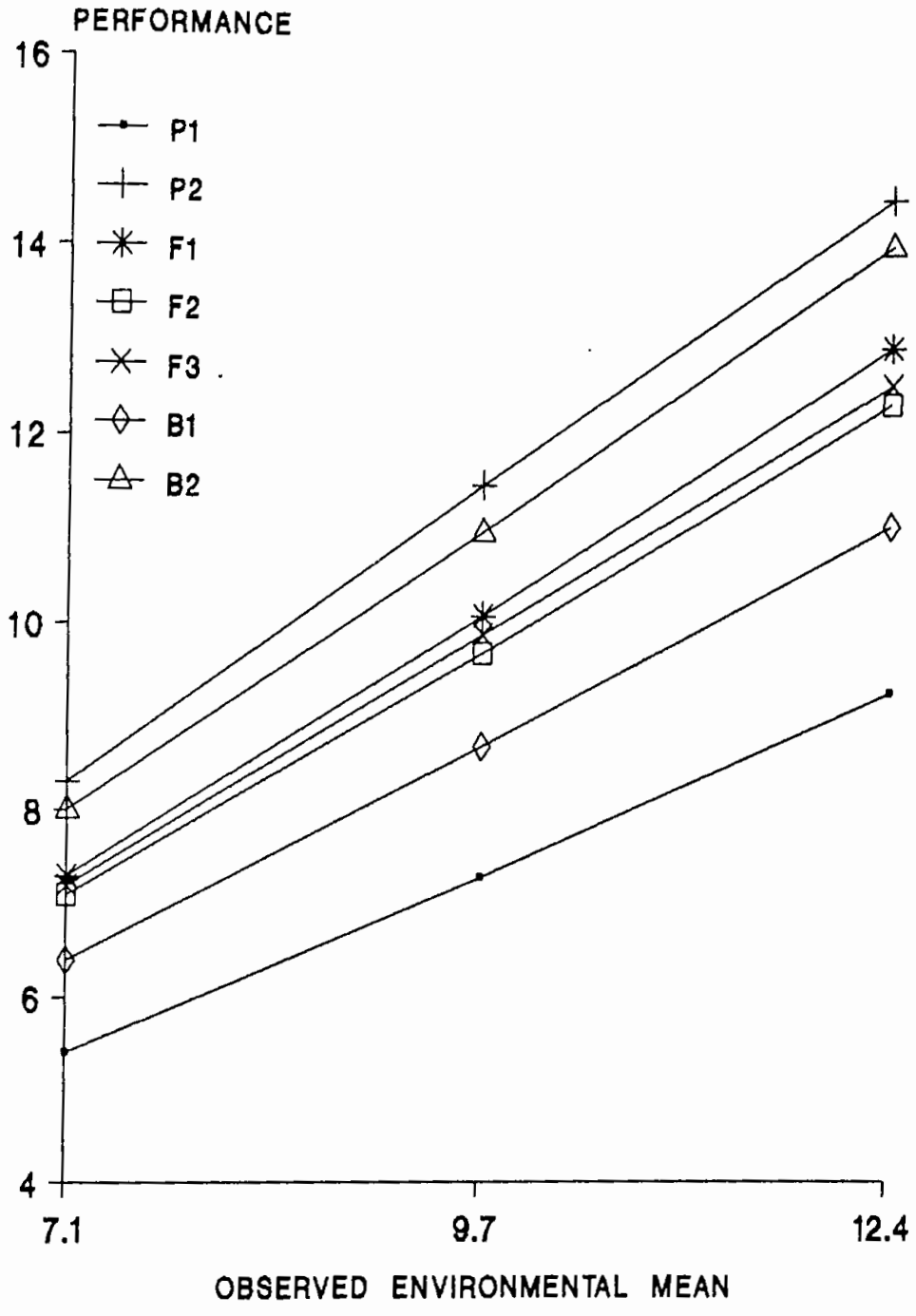

Fig. 7. Regression of different populations on means of primary branches per panicle under eight different environments.

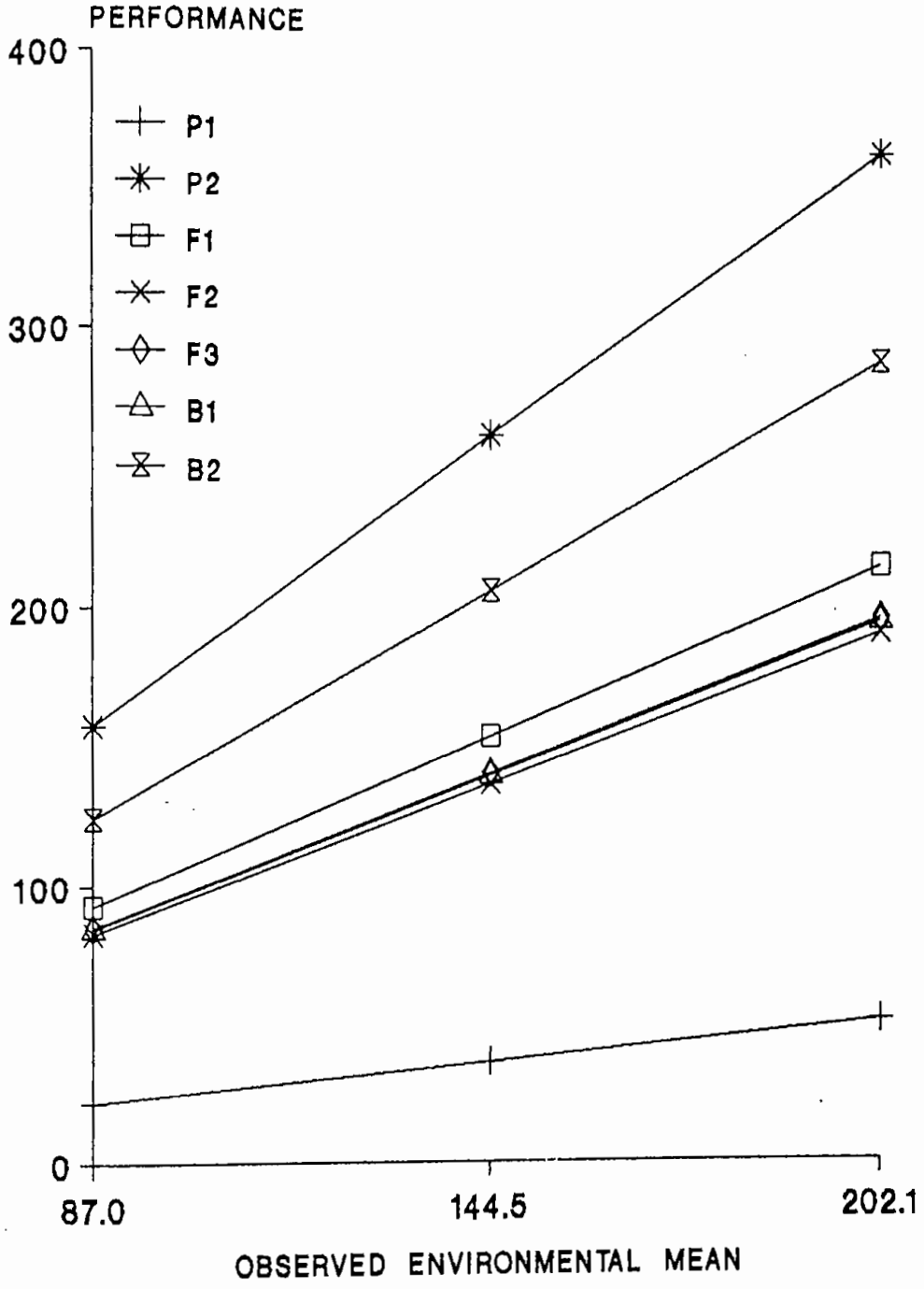

Fig. 8. Regression of different populations on means of grains per panicle under eight different environments.

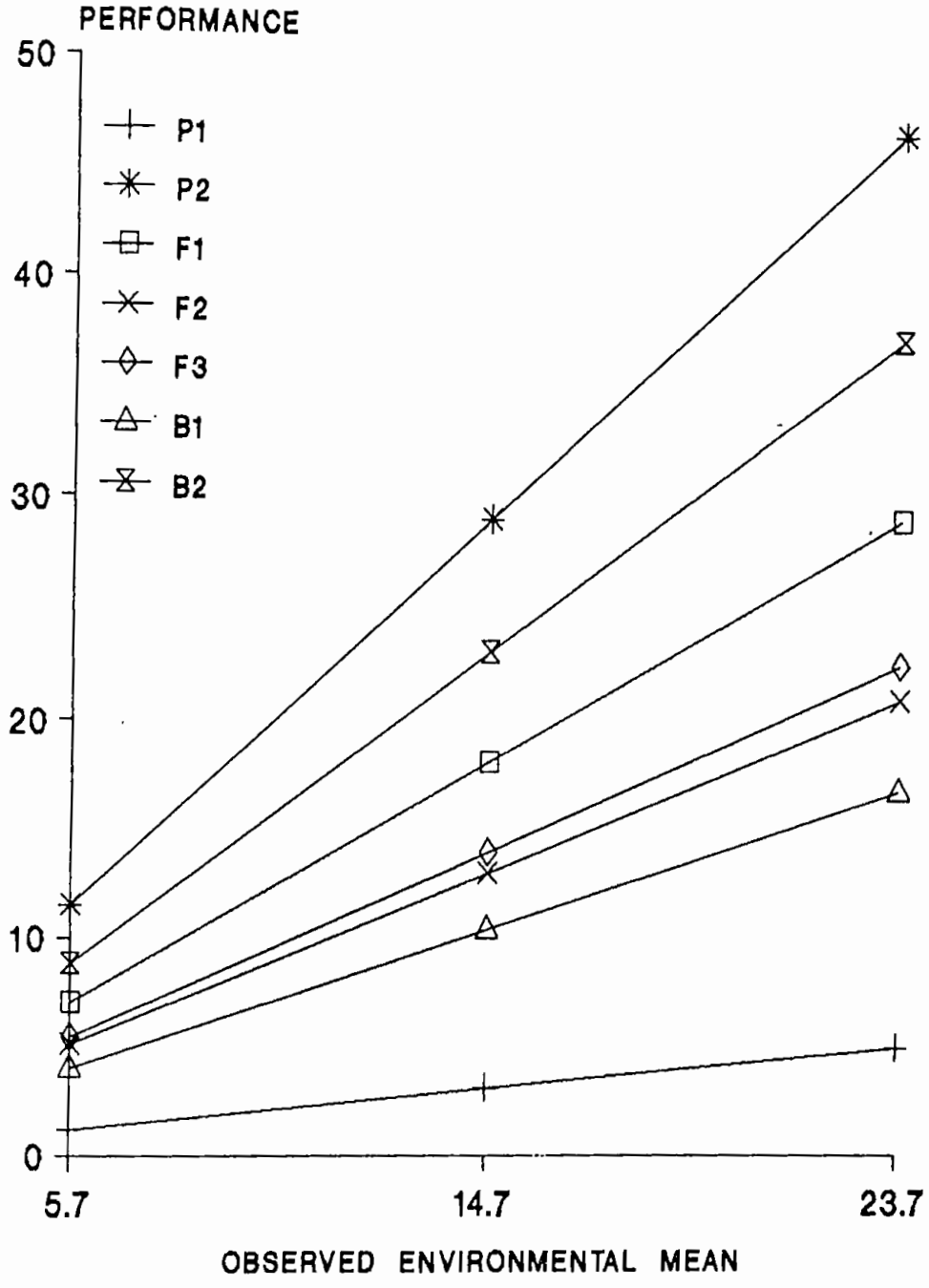

Fig. 9. Regression of different populations on means of grain yield per plant under eight different environments.

Table-6

Correlation co-efficient (r) between means ($\bar{X}$) and responses (b_i); between means($\bar{X}$) and stabilities ($\bar{S}^2_d$) and between responses (b_i) and stabilities ($\bar{S}^2_d$) within characters.

	Between $\bar{X}$ and b_i	Between $\bar{X}$ and ($\bar{S}^2_d$)	Between b_i and ($\bar{S}^2_d$)
Plant height	0.99**	-0.58	-0.61
Effective tillers/ plant	0.98**	0.17	0.24
Panicle length	0.94**	0.68	0.84*
Flag leaf length	0.94**	0.03	-0.12
Flag leaf breadth	0.99**	-0.52	-0.39
Flag leaf area	0.99**	0.25	0.12
Primary branches/ panicle	0.99**	0.02	0.01
Grains/panicle	1.00**	0.52	0.52
Grain yield/plant	1.00**	0.38	0.37

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

Table-7

Correlation co-efficients (r) between means ($\bar{X}$), between responses (b_i) and between stabilities ($\bar{S}^2_d$) of different characters.

	PH	ET/P	PL	FLL	FLB	FLA	PB/P	G/P	Gy/P
Between means ($\bar{X}$) :									
PH	-	0.87*	0.92**	0.96**	0.95**	0.94**	0.95**	0.96**	0.94**
ET/P		-	0.98**	0.95**	0.98**	0.94**	0.94**	0.96**	0.98**
PL			-	0.95**	0.98**	0.94**	0.96**	0.96**	0.99**
FLL				-	0.98**	0.97**	0.94**	0.99**	0.96**
FLB					-	0.98**	0.97**	0.99**	0.99**
FLA						-	0.94**	0.97**	0.96**
PB/P							-	0.96**	0.98**
G/P								-	0.96**
Gy/P									-
Between responses (b_i) :									
PH	-	0.77*	0.84*	0.75	0.86*	0.90**	0.94**	0.96**	0.93**
ET/P		-	0.93**	0.93**	0.98**	0.86*	0.92**	0.89**	0.94**
PL			-	0.84*	0.94**	0.96**	0.94**	0.94**	0.96**
FLL				-	0.94**	0.81*	0.86*	0.84*	0.88**
FLB					-	0.92**	0.94**	0.94**	0.97**
FLA						-	0.90**	0.96**	0.93**
PB/P							-	0.96**	0.99**
G/P								-	0.97**
Gy/P									-

Continued overleaf

Table-7 (Continued)

Correlation co-efficients (r) between means ($\bar{X}$), between responses (b_i) and between stabilities ($\bar{S}^2_d$) of different characters.

	PH	ET/P	PL	FLL	FLB	FLA	PB/P	G/P	Gy/P
Between stabilities ($\bar{S}^2_d$) :									
PH	-	-0.12	0.33	-0.14	0.58	0.07	0.07	-0.18	0.64
ET/P		-	-0.18	-0.71	0.45	0.92**	0.25	-0.14	-0.20
PL			-	0.21	-0.14	0.03	0.07	0.34	0.93**
FLL				-	-0.26	-0.63	-0.39	0.46	0.12
FLB					-	0.57	0.30	-0.41	0.14
FLA						-	0.12	-0.06	0.06
PB/P							-	-0.88**	-0.01
G/P								-	0.17
Gy/P									-

* and ** Indicate Significant at 5% and 1% levels, respectively.

PH = Plant height
ET/P = Effective tillers/plant
PL = Panicle Length
FLL = Flag leaf length
FLB = Flag leaf breadth
FLA = Flag leaf area
PB/P = Primary branches/panicle
G/P = Grains/panicle
Gy/P = Grain yield/plant

Table-8

Estimates of m, d and h based on 3-parameter model (unweighted analysis) for different characters.

	m	d	h	$\chi^2_{(df=4)}$
PH	96.97 ± 4.45	-19.96 ± 4.73	12.74 ± 8.74	111.95***
ET/P	6.74 ± 0.17	-0.88 ± 0.18	0.23 ± 0.33	0.16
PL	22.70 ± 0.20	-1.18 ± 0.21	0.45 ± 0.39	0.23
FLL	29.85 ± 0.68	-2.84 ± 0.73	1.18 ± 1.34	2.63
FLB	1.30 ± 0.02	-0.09 ± 0.02	0.04 ± 0.03	0.002
FLA	26.59 ± 1.00	-4.50 ± 1.07	1.36 ± 1.97	5.69
PB/P	9.16 ± 0.08	-1.10 ± 0.08	0.29 ± 0.15	0.03
G/P	132.09 ±10.76	-52.30 ±11.44	20.33 ±21.15	654.83***
Gy/P	13.15 ± 0.59	-6.58 ± 0.62	2.23 ± 1.15	1.94

*** Indicate significant at 0.1% level

PH = Plant height
ET/P = Effective tillers/plant
PL = Panicle Length
FLL = Flag leaf length
FLB = Flag leaf breadth
FLA = Flag leaf area
PB/P = Primary branches/panicle
G/P = Grains/panicle
Gy/P = Grain yield/plant

Table-9

Estimates of m, d and h and their three types of gene interaction (i, j and l) based on 6-parameter model (unweighted analysis) for plant height and grains per panicle.

	Plant height	Grains per panicle
m	102.20 ± 6.32	113.70 ± 19.04
d	-22.40 ± 2.21	-57.95 ± 6.67
h	12.33 ± 19.27	98.21 ± 58.11
i	-8.03 ± 6.41	15.16 ± 19.33
j	24.40 ± 9.89	56.50 ± 29.81
l	-7.94 ± 14.85	-67.29 ± 44.77

Table 10

Effect of N, P, K and their different combinations on different characters performed by the populations.

	N	P	K	NP	NK	PK	NPK
PH	123.43***	29.65***	16.85***	4.71	1.79	2.01	2.07
ET/P	13.04***	2.82***	1.50***	1.48***	0.24	0.62	0.60
PL	28.48***	6.66***	3.50**	1.32	0.48	0.10	0.04
FLL	36.35***	9.19***	5.49	1.67	1.21	0.41	0.57
FLB	1.18***	0.32***	0.22***	-0.04	-0.02	0.04	0.08
FLA	55.08***	14.72***	9.84***	2.44	2.28	2.72	3.16
PB/P	13.68***	4.74***	2.14***	1.44**	1.08	1.02	0.80
G/P	360.45***	61.33***	31.65***	20.91***	7.43	7.35	7.17
Gy/P	60.06***	7.99***	3.34***	3.94***	0.94	-0.14	0.46

** and *** Indicate significant at 1% and 0.1% levels, respectively.

PH = Plant height
ET/P = Effective tillers/plant
PL = Panicle Length
FLL = Flag leaf length
FLB = Flag leaf breadth
FLA = Flag leaf area
PB/P = Primary branches/panicle
G/P = Grains/panicle
Gy/P = Grain yield/plant

Table-11

Effect of N, P, K and their different combinations on different characters of different populations.

	N	P	K	NP	NK	PK	NPK
Plant height :							
P_1	90.49***	20.83***	13.17***	4.17	1.83	1.49	1.51
P_2	139.16***	33.50***	19.50***	4.84	2.86	3.18	3.16
F_1	130.16***	31.50***	17.84***	5.18	2.84	2.38	2.50
F_2	128.00***	31.20***	17.80***	5.40	2.40	2.40	2.20
F_3	129.36***	31.04***	18.02***	5.22	2.64	1.56	2.38
B_1	122.84***	29.18***	16.84***	5.18	2.16	2.50	2.50
B_2	135.82***	32.50***	18.84***	4.84	2.50	2.50	2.84
Effective tillers/plant :							
P_1	11.50***	2.50***	1.50***	1.18***	0.18	0.50	0.50
P_2	14.67***	3.01***	1.67***	1.67	0.33	0.67	0.65
F_1	13.54***	2.80***	1.54***	1.52	0.14	0.88**	0.80*
F_2	12.50***	2.90***	1.30***	1.50	0.30	0.70	0.50
F_3	12.30***	2.70***	1.30***	1.30	0.30	0.70	0.50
B_1	12.50***	2.82***	1.50***	1.50	0.18	0.50	0.50
B_2	13.99***	2.99***	1.67***	1.65	0.33	0.65	0.67

Continued overleaf

Table-11 (Continued)

Effect of N, P, K and their different combinations on different characters of different populations.

	N	P	K	NP	NK	PK	NPK
Panicle length :							
P_1	26.33***	6.67***	3.33**	1.33	0.67	0.33	-0.33
P_2	30.18***	6.50***	3.84***	1.50	0.16	-0.16	0.16
F_1	28.98***	6.34***	3.66***	1.66	0.34	0.34	-0.34
F_2	28.10***	6.70***	3.30**	1.56	0.70	0.10	0.10
F_3	28.50***	6.70***	3.30**	1.30	0.70	0.10	-0.10
B_1	27.83***	6.83***	3.51***	1.17	0.49	0.17	-0.17
B_2	29.50***	6.82***	3.50***	1.18	0.50	-0.18	0.82
Flag leaf length :							
P_1	31.83***	8.17***	4.83	1.83	1.17	0.83	0.49
P_2	39.84***	10.16***	5.84*	1.82	1.50	0.50	0.16
F_1	37.01***	9.33***	5.67	1.67	1.33	0.33	0.67
F_2	36.70***	9.30***	5.70*	1.70	1.30	0.30	0.70
F_3	36.20***	9.00***	5.60	1.40	1.20	0	0.40
B_1	34.48***	8.49***	5.83*	1.49	0.83	0.17	0.49
B_2	38.24***	10.00***	5.34	1.66	1.00	0.66	1.00

Continued overleaf

Table-11 (Continued)

Effect of N, P, K and their different combinations on different characters of different populations.

	N	P	K	NP	NK	PK	NPK
Flag leaf breadth :							
P_1	1.01***	0.29***	0.21***	-0.01	-0.07	0.01	0.11
P_2	1.31***	0.37***	0.25***	-0.07	-0.03	0.03	0.07
F_1	1.16***	0.34***	0.26***	-0.04	0.04	0.06	0.08
F_2	1.15***	0.33***	0.21***	-0.03	-0.03	0.03	0.07
F_3	1.15***	0.31***	0.21***	-0.05	-0.03	0.05	0.09
B_1	1.14***	0.30***	0.22***	-0.04	0	0.04	0.10
B_2	1.23***	0.35***	0.25***	-0.05	-0.03	0.05	0.05
Flag leaf area :							
P_1	43.52***	11.73***	7.14***	2.51	1.12	1.73	2.54
P_2	65.81***	17.64***	12.03***	2.02	2.23	2.22	1.82
F_1	54.13***	15.52***	10.92***	2.73	3.34	5.91*	6.33*
F_2	54.64***	15.81***	10.21***	3.44	3.21	1.04	1.61
F_3	55.21***	15.03***	9.84***	2.41	2.02	2.62	2.84
B_1	54.63***	14.22***	16.43***	2.02	2.23	2.23	2.02
B_2	57.04***	15.24***	9.42***	2.83	2.24	2.81	4.03

Continued overleaf

Table-11 (Continued)

Effect of N, P, K and their different combinations on different characters of different populations.

	N	P	K	NP	NK	PK	NPK
Primary branches :							
P_1	11.84***	4.16***	1.50***	1.18*	1.16*	0.67	0.50
P_2	14.66***	5.34***	2.32***	1.34**	1.00	1.00	1.00
F_1	13.83***	5.03***	2.17***	1.17*	1.19*	0.83	1.17*
F_2	13.40***	4.80***	2.00***	1.40***	1.40***	0.80	1.00
F_3	13.70***	4.90***	2.10***	1.50***	1.10*	1.10*	0.90
B_1	12.83***	4.51***	1.83***	1.17*	1.17*	0.85	0.83
B_2	14.50***	5.16***	2.18***	1.50***	1.16*	1.18*	0.84
Grains/panicle :							
P_1	182.01***	32.80***	13.62***	12.83***	1.64	1.20	1.21
P_2	475.70***	78.11***	45.53***	24.14***	13.50***	13.71***	13.32***
F_1	370.72***	60.92***	35.74***	18.70***	9.91***	10.92***	9.93***
F_2	349.03***	56.43***	34.80***	16.81***	10.82***	10.23***	10.64***
F_3	355.24***	59.24***	31.81***	19.82***	8.63*	8.04*	7.20
B_1	356.50***	63.30***	27.52***	24.53***	3.50	3.50	3.51
B_2	433.41***	77.22***	33.43***	28.84***	4.81	4.81	5.22

Continued overleaf

Table-11 (Continued)

Effect of N, P, K and their different combinations on different characters of different populations.

	N	P	K	NP	NK	PK	NPK
Grain yield/plant :							
P_1	27.66***	3.0***	2.00	2.00	1.00	-0.34	-0.02
P_2	82.15***	12.17***	2.83***	7.51***	0.17	2.83***	2.17*
F_1	66.98***	9.34***	3.34***	4.66***	0.66	-0.34	0.34
F_2	56.70***	7.50***	2.90***	3.50***	0.90	-0.30	0.50
F_3	58.90***	1.90***	3.10***	3.90***	0.70	-0.30	0.50
B_1	50.37***	7.03***	3.03***	3.31***	0.63	-0.03	0.37
B_2	75.67***	10.67***	3.67***	4.99***	1.35	-0.33	0.67

*, ** and *** Indicate significant at 5%, 1% and 0.1% levels, respectively.

DISCUSSION

The occurrence of genotype-environment interaction has long been provided a major challenge to obtain a fuller understanding of genetic control of variability. The study of genotype-environment interaction in its biometrical aspect is important, not only from genetical and evolutionary points of view, but also very relevant to the production problem of agriculture in general and to plant breeding in particular (Breese, 1969). A knowledge of the nature and relative magnitude of the various types of genotype-environment interaction is thus important in making decisions concerning breeding methods, selection programmes and testing procedures in crops. Plant breeders are well aware of the problems regarding genotype-environment interaction in breeding better varieties but until recently there was no agreement about its analytical approaches. Recently two approaches have been made to study the genotype-environment interaction. The first approach is purely statistical (Yates and Cochran, 1938; Finlay and Wilkinson, 1963; Eberhart and Russell, 1966) and the second approach is based on the biometrical genetics (Jinks, 1954; Jinks and Mather, 1955; Mather and Jones, 1958; Bucio Alanis, 1966; Bucio Alanis and Hill, 1966; Perkins and Jinks, 1968a). Both the analyses gave similar results which show that genotype-environment component is often a linear function of the environmental means. In the present study, a major part of the

genotype-environment interaction both in segregating (F_2, F_3, B_1 and B_2) and non-segregating (F_1 and parents) generations was accounted for by the linear function of the environmental means, although very smaller and non-significant part was non-linear and independent of this linear component in all the characters.

A plant breeder pins his hope for crop improvement upon evidence of genetic variation for the character being selected. Accurate estimates of the genetic variance will be obtained only if such estimates are unbiased by variation owing to G X E interactions. Unbiased estimates of genetic and G X E components of variance can be readily obtained by equating the expected mean squares with those calculated from the experiment. Significant G X E interactions suggested that significant differences existed between the different generations interacted with the environments. This also indicated that G X E interactions were operative in the characters under study.

Population means of different segregating (F_2, F_3, B_1 and B_2) and non-segregating (F_1 and parents) generations varied within and between environments. The means of cross populations were within the parental ranges. The variation of mean performance between the generations was an indication of genetic diversity of the different generations. Estimates of environmental means indicated that different environments had different effects on the different characters of the populations considered. All the segregating and non-segregating populations

for all the characters were greatly affected by the different nutritional treatments. It was, however, observed that nitrogen treatment either singly or in combination with others, always increased the phenotypic means of all the characters of all the generations. On the other hand, the treatment zero ($N^-P^-K^-$) or the treatment phosphate and potash, either singly or in combination with others, decreased the magnitude of the phenotypic means in majority of the cases. Pearman *et al.* (1978), Islam (1978), Whingwiri and Kemp (1980) and many other investigators reported the higher effects of nitrogen (N) on yield and other characters of wheat. Effect of N on different characters of rice was also reported by Uddin *et al.* in 1979. It was evident from the nutritional effects that a wide range of environments gave ample opportunity for the manifestation of genotype-environment interaction.

Analysis of variance showed that the items population (P), environment (E) and year (Y) were highly significant in all the traits indicating that real differences existed between the populations, between the effects of different environments and between year effects. Among the interactions real differences were found in case of P X E in all the characters, in case of P X Y in five characters and in case of P X E X Y in seven characters. The varied mean squares of P X E revealed that different characters of the populations interacted differently with the environments.

During the joint regression analysis linear relationships of the populations with the environments were found to be present in all the characters. It was also observed that the linear relationships of all the populations in all the characters were significant when tested with error or deviation mean squares and non-linear relationships were non-significant when tested with error mean squares. This indicated that in all cases the populations had significantly greater proportion of linear relationships compared to the non-linear relationships with environments i.e. greater influence of environments were present on the characters of the populations. The linear and non-linear relationships of different crops with environments have been shown by many investigators such as Yates and Cochran (1938), Finlay and Wilkinson (1963), Eberhart and Russel (1966), Bucio Alanis (1966), Perkins and Jinks (1968a and 1968b), Freeman and Perkins (1971) and Frip and Caten (1973). In recent years, Widner and Lebsock (1973), Bains (1976), Islam (1978), Jatasra and Paroda (1979) Singh and Singh (1980), Islam *et al.* (1981) and Parh and Khan (1986 and 1987) have also detected linear and non-linear relationships with environments of different wheat genotypes. In rice also Khaleque (1975), Khaleque and Eunus (1977), Uddin *et al.* (1979), Azam (1981), Amirthadevarathinam (1987), Alfonso (1988), Ganesh and Soundrapandian (1988) and Narendra *et al.* (1988) have found linear and non-linear relationships were operative in different quantitative characters

of different genotypes with environments. The test of linear regression with deviation mean square further indicated that significant linear variations were independent of their respective non-linear variations of genotype-environment interaction. It also suggested that both linear function or response and non-linear function or stability of environment are under the control of different gene systems (Perkins and Jinks, 1968b).

Different measures of stability have been used by various workers. Earlier, Finlay and Wilkinson (1963) considered linear regression slopes as a measure of stability. Eberhart and Russel (1966) defined the linear and non-linear function of genotype-environment interactions as "Stability parameters", β_i (Linear regression, b_i) and $\bar{S}_d^2$ (deviation from regression) respectively. They also emphasized that the phenotypic expression of a particular genotype under a specific environment depend on the mean expression (μ_i), the linear response of the genotype to change of the environment (β_i) and the extent of residual deviation from regression (σ_{ij}). Later, Breese (1969), Samuel *et al.* (1970), Paroda and Hayes (1971) and Jatasra and Paroda (1978) emphasized that the linear regression could simply be regarded as a measure of response of a particular genotype, whereas, the deviation around the regression line ($\bar{S}_d^2$) is the most suitable measure of stability and genotypes with the lowest standard error (Sb_i) or deviation around the regression line being the most

stable and vice versa. Accordingly, it was possible to judge the stability of genotypes and due consideration was also given to their mean performances and linear responses. They proposed that the criteria for stability should be regression coefficient (b_i) of unity and a minimum $\bar{S}^2_d$. A cultivar with high mean yield and fulfilling the above two criteria would perform well in all environments. In the light of these statements it may be concluded that first a genotype for a particular character having high mean performance ($\bar{X}$), average regression coefficient (b_i) and low $\bar{S}^2_d$ value will be suitable under favourable environments. Secondly, the genotype having comparatively low b_i and $\bar{S}^2_d$ value with moderately high mean performance will be specially adopted to low yielding environments. These genotypes are so insensitive that they are unable to exploit high yielding environments. Lastly, the genotype that have low mean performance, b_i and $\bar{S}^2_d$ will be consistently low yielders under all environments. However, the genotypes which have high $\bar{S}^2_d$ yet they deserve inclusion to suitable environments because of the presence of high b_i and high mean performances and these genotypes are very sensitive to environmental changes.

In the present experiment, most of the genotypes of segregating and non-segregating generations had significant response (b_i) for all the characters which indicated that the linear component contributed to most of the total genotype-environment interaction. This information is in confirmity with

the one obtained from joint regression analysis. The range of b_i values of the segregating and non-segregating generations (F_1, F_2, F_3, B_1 and B_2) did not exceeded the parental range in any of the cases which indicated that this aspect of phenotype was simply inherited. All the b_i values of P_1 and B_1 generations were below the average response while those values of P_2 and B_2 generations were above the average response and the b_i values of F_1, F_2 and F_3 generations were near the average response in all the cases. The results suggested that the b_i values were heterogeneous in all the cases. Wide range and great diversity were met with these b_i values as revealed by Bartlett's Homogeneity Test indicating the presence of great genetic diversity among the populations in the amount of linear relationship with the environment. It also suggested that the genotypes had their own intrinsic variation and this attribute is under gene control. On the other hand, all the populations showed more or less similar performance for non-linearity or stability. The stability estimates ($\bar{s}_d^2$) did not vary much in a particular character. Linear function of different genotypes have been reported earlier by many investigators such as Finlay and Wilkinson (1963) in Barley, Eberhart and Russel (1966) in Maize, Perkins and Jinks (1968a) in Nicotiana. In wheat also many workers such as Widner and Lebsock (1973), Bains (1976), Islam (1978), Chaudhary and Paroda (1979), Jatasra and Paroda (1979), Singh and Singh (1980), Islam *et al.* (1981) and Parh and Khan

(1987 and 1988) have reported linear functions of different genotypes for grain yield and different agronomic characters. Linear function of different genotypes for different characters in rice have also been reported in recent years by many scientists such as Khaleque and Eunus (1977), Uddin *et al.* (1979), Azam (1981), Amirthadevarathinam (1987), Ganesh and Soundrapandian (1988) and Narendra *et al.* (1988). In the present study non-linear functions or stability estimates were found to be very low and non-significant compared to the linear functions or responses of different characters of different genotypes. The relative proportions of stability estimates for parents and cross populations suggested that non-linear component contributed to some extent in the genotype-environment interaction of these characters. These results coincide partly with the results of Khaleque and Eunus (1977), Uddin *et al.* (1979), Azam (1981), Amirthadevarathinum (1987) and Ganesh and Soundrapandium (1988). They found both linear and non-linear functions were operative of which linear function predominantly contributed to the G X E interaction of different characters of different genotypes in rice.

From the results it was observed that among the parents and cross populations, parent Mut NS1 had high response (b_1) with high mean and low stability in all the characters which indicated its suitability for favourable environments. On the other hand, the cross populations F_1, F_2 and F_3 generations had more or less

unit response, moderate high mean and low stability in all the characters which indicated their suitability for all environments. Thus selection from the segregating generations (F_2 and F_3) for all environments will be more effective. Azam (1981), Amirthadevarathinam (1987), Narendra *et al.* (1988) and Ganesh and Soundrapandian (1988) made selections on the basis of $\bar{X}$, b_i and $\bar{S}^2_d$ for different environments for grain yield and other characters in rice.

The correlation between mean ($\bar{X}$) and response (b_i) of all the characters were found highly significant and positive in nature indicating that response is directly proportional to population mean of the genotypes i.e. response of population increases with the increase of mean. This also indicated that these two aspects of phenotype are under the control of same gene system. Eberhart and Russel (1966), Perkins and Jinks (1968a), Westerman (1971), Bush *et al.* (1976) and Singh and Singh (1980) reported positive correlations between these three aspects ($\bar{X}$, b_i and $\bar{S}^2_d$) of phenotype. On the other hand, correlations between mean ($\bar{X}$) and stability ($\bar{S}^2_d$) and between response (b_i) and stability ($\bar{S}^2_d$) whether positive or negative were found to be non-significant in most cases. This suggested that stability is independent of the other two aspects (mean and response) of phenotype and it is under the control of different gene system. The independent nature of stability or non-linearity from response or linearity was also indicated by joint regression

analysis. The independent nature of these three aspects ($\bar{X}$, b_i and $\bar{S}^2_d$) of phenotype in different crops was reported by many workers such as Khaleque, 1975; Bush *et al.*, 1976; Uddin *et al.*, 1979 and Uddin, 1983.

Significant positive association of means of different characters in all the cases suggested that mean performance (either increase or decrease) of any character is dependent on the mean performances (either increase or decrease) of other characters. The association of responses of different characters in all the cases, except one, gave similar results. On the other hand, the insignificant association, either positive or negative, between stabilities in most of the cases suggested that stability parameters of the characters are independent of stability parameters of other characters. The significant association between means and between responses supports foregoing discussion that means and responses are controlled by same gene systems.

Regarding the genetic control of means ($\bar{X}$) of different characters, the data of this study confirmed the observation and genetic architecture presented in the PART I of this Thesis. Additivity, dominance and non-allelic gene actions were found from the present data. Significant additive effects (d) and non-significant dominance (h) effects suggested that additive genes compared to dominance genes contributed a major part in the inheritance of these characters. Non-allelic gene action or epistasis was observed in case of plant height and grains per

panicle. Opposite signs of 'h' and 'l' in these two characters suggested the involvement of duplicate type of gene action in these cases. These results also confirmed our results presented in PART I.

Results obtained from the estimation of effect of different fertilizers and their combinations on different characters indicated that the fertilizers (N, P and K) singly had significant single effect on all the characters except K on flag leaf length. The nature of these effects were positive suggesting that plants receiving these three fertilizers singly had increased performance of grain yield and other characters. Significant positive effect of N in combination with P was also observed in effective tillers per plant, primary branches per panicle, grains per panicle and grain yield per plant. However, the effect of N application was much more greater than the effects produced by other fertilizers. Similar types of results were obtained by Khaleque and Eunus (1977), Uddin *et al.* (1979) and Azam (1981) in grain yield and yield components of rice. Favourable effect of N application have also been reported by Uddin *et al.* (1980) in root-shoot characters of rice.

Results of effects of different fertilizers and their combinations on different characters of different populations also showed more or less similar results. All the characters of different populations were affected by the fertilizers when applied singly. These fertilizers, when applied singly, produced

favourable and significant effect on the characters of different populations except the case of flag length of P_1, F_1, F_3 and B_2 and grain yield/plant of P_1. The combination of N with P significantly affected primary branches per panicle, grains per panicle and yield per plant of most of the populations. Few of the studied characters of some of the populations have been affected by the other combinations of N, P and K.

From the foregoing discussion it becomes evident that high mean performance of grain yield and other eight different characters have been inherited from the mutant lines to their cross generations and the characters of these populations were highly stable with response near to unity. This suggested their suitability for all environments. The discussion also indicated that additivity played the major role in the inheritance of these means of different characters. The use of these mutant lines in future breeding programme is, therefore, highly desirable.

SUMMARY

An investigation on genotype-environment interaction was carried out for nine agronomic characters of rice (*Oryza sativa* L.) involving segregating (F_2, F_3, B_1 and B_2) and non-segregating (F_1 and parents) generations under eight artificially created soil environments with N, P and K fertilizers. It also included the study of relationship between three parameters viz., mean ($\bar{X}$), response (b_1) and stability ($\bar{s}^2_d$) of a phenotype and a genetic nature of mean. Means of different segregating and non-segregating generations were different for different characters. These means varied within and between environments. The means of cross populations were within the parental ranges. Environmental means indicated that means of all the characters of the populations were greatly affected by the different nutritional treatments.

Genotype-environment interactions were found to be operative in both segregating and non-segregating generations. Linear functions of the interactions were significant suggesting that major part of the interactions were accounted by the linear functions of the environmental means. However, some of the interactions were accounted by the non-linear functions which were independent of the linear functions of the environmental means. Both linear and non-linear components of genotype-environment interaction were under the control of different gene

systems. The genotypes had varied responses to environmental changes. The range of responses among the segregating and non-segregating generations (F_1, F_2, F_3, B_1 and B_2) did not exceed the parental ranges in both the directions in all the cases. For different characters average, below average and above average responses were exhibited by the different genotypes and the standard errors of responses were heterogeneous. All the genotypes showed more or less similar stability in all the characters. Joint regression analysis gave the similar indication. Selections for all environments can be made from the segregating generations (F_2 and F_3). Correlation studies of three aspects viz., mean, response and stability ($\bar{X}$, b_1 and $\bar{S}^2_d$) of phenotype indicated that response is dependent and stability is independent of the means. It also indicated that mean and response are controlled by same genes system while stability is controlled by different gene systems.

Nature of inheritance of mean was detected and estimated. It was found that additivity played the major part in the inheritance of mean of all the characters. Duplicate types of gene actions were also noted in two of the studied characters.

Individual application of fertilizers (N or P or K) had favourable effects on all the characters of the populations. Application of N, compared to the other fertilizers or different combinations of these three fertilizers, had the greatest effect on the studied characters.

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