

**INVESTIGATION ON ADDITIVE, DOMINANCE AND
EPISTATIC VARIATION FOR AGRONOMIC TRAITS
IN WHEAT** (*Triticum aestivum* L.)

THESIS

SUBMITTED TO

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**Doctor of Philosophy
in
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By

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Dedicated to the

Everlasting Memory of my Mother

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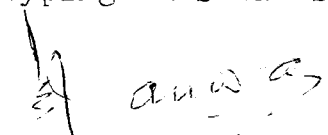
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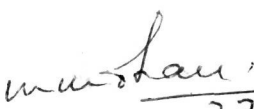

(K.S. PANWAR)

CERTIFICATE I

This is to certify that this thesis entitled, "Investigation on additive, dominance and epistatic variation for agronomic traits in wheat (Triticum aestivum L.)", submitted for the degree of Doctor of Philosophy, in the subject of Plant Breeding and Genetics of the Himachal Pradesh Krishi Vishva Vidyalaya, Palampur, is a bonafide research work carried out by Shri Khazan Singh Panwar, under my supervision and that no part of this thesis has been submitted for any other degree.

The assistance and help received during the course of this investigation have been duly acknowledged.

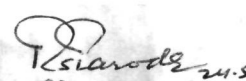
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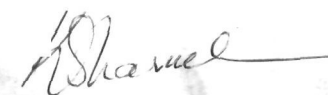

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CERTIFICATE II

This is to certify that the thesis entitled "Investigation on additive, dominance and epistatic variation for agronomic traits in wheat (Triticum aestivum) L.", submitted by Sh. Khazan Singh Panwar to the Himachal Pradesh Krishi Vishva Vidyalaya in Partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Subject of Plant Breeding and Genetics has been approved by the Student's Advisory Committee, after an oral examination on the same, in collaboration with an External Examiner.


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Chapter I

INTRODUCTION

Wheat (Triticum aestivum L.) is one of the most important food crops in the world. In India, a significant varietal improvement has been made and a number of high yielding varieties released. However, now a kind of plateau has been arrived at in the per se yielding capacity of these varieties and the improvement is being made in characters like disease resistance and quality. More concerted efforts are needed for the genetic upgrading of this important crop to develop cultivars that excel the existing ones both in productivity and quality.

The incorporation of superior qualitative characters in the cultivars has long enjoyed effective genetic guidance and, therefore, such programmes are accurate and predictable. On the other hand, improvement in the quantitative characters has exhibited a limited progress till the advent of the Fisher-Yates-Mather-Jinks-Hayman diallel technique, which was hailed by plant breeders as a long overdue methodology for rationalizing the genetic study of continuous variation (Johnson, 1963).

The information on the nature of gene action governing particular characters is not only important but essential for

formulating any plant breeding programme. Analysis of genetic architecture is the starting step for proper management of genetic variability for such traits. Thus the choice of most suitable breeding procedure, among several available, would depend to a large extent on the nature of gene action involved in the control of character or characters in which the plant breeder is interested.

Till recently, different biometrical approaches have been applied to explore the genetic architecture of this crop and a spectacular improvement obtained mostly by the exploitation of additive genetic variance. However, a majority of the populations remain to be investigated further for channelizing them in the population improvement programmes. Of the many genetic models used, the most widely adopted mating designs for the estimation of genetic variance and its components are diallel cross techniques (Jinks and Hayman, 1953; Hayman, 1954 a,b; Griffing, 1956; Gardner and Eberhart, 1966), generation means analyses (Anderson and Kempthorne, 1954; Jinks and Jones, 1958; Hayman, 1958), partial diallel cross (Kempthorne and Curnow, 1961; Hinkelmann and Stern, 1960; Hinkelmann, 1965), line x tester analysis (Kempthorne, 1957), triallel analysis (Rawlings and Cockerham, 1962; Ponnuswami, 1972) and partitioning of variances through bi-parental progenies (Comstock and Robinson, 1952; Matzinger and Cockerham, 1963).

The use of most of these mating designs envisages the tremendous increase in the number of crosses with an increase in the number of parents. Making of a large number of crosses and their evaluation in field experiments becomes cumbersome and unmanageable, especially when the breeder intends to study the genetic architecture of a fairly large number of genotypes. Furthermore, the restrictions of the genetic model in these analyses do not permit the unbiased computation of all the genetic parameters.

An experimental method overcoming these limitations has been developed by Kearsey and Jinks (1968) and is known as triple test-cross. The triple test-cross which is an extension of North Carolina Design III of Comstock and Robinson (1952), is the most recent among the different mating designs available for conducting genetic analysis. This design has a number of advantages over other designs since it provides precise and independent tests for the estimates of various genetic parameters together with a test for the detection of epistasis, which is not possible in most of the other multiple mating designs. Furthermore, this method is general because it is applicable to any population, irrespective of its gene and genotypic frequencies and breeding system. For a population of pure breeding lines, as in the case of wheat the triple test-cross of Kearsey and Jinks (1968) has been modified by making crosses of $i = 1$ to n samples of genotypes with three

testers of which two testers, L_1 and L_2 are phenotypic extreme genotypes, whereas the third tester, L_3 , is an F_1 between L_1 and L_2 . The L_{3i} progeny families in the simplified triple test-cross of Jinks, Perkins and Breese (1969) are replaced by P_i , pure breeding lines themselves in order to provide a test for the simple model. The P_i pure breeding families and L_{3f} progeny families when grown simultaneously provide two tests of the simple model as suggested by Jinks and Virk (1977) and the comparison of these two tests provides the basis of detection of any bias, due to common genes, if any, in the two pure breeding testers (Virk and Jinks, 1977). The method also allows detection of interactions between genotypes and the micro- and macro-environments (Perkins and Jinks, 1971).

In the investigations reported here, an attempt has been made to evaluate a random sample of wheat homozygous lines, keeping in view the above considerations with the following objectives :

- i) to gather information on the amount and magnitude of additive, dominance and epistatic variances for yield and other traits of economic importance
- ii) to formulate breeding methodology for the utilization of the information obtained, for further improvement in wheat in general and in this material in particular

Chapter II

REVIEW OF LITERATURE

The information on the genetic systems controlling quantitative characters is essential for the initiation of an effective and efficient selection procedure. The different breeding programmes are built on the basic knowledge of genetic make up and nature of gene action, which largely have accumulated through the exploitation of :

- 1 Additive genetic variance
- 2 Dominance variance
- 3 Epistatic variance
- 4 Average degree of dominance, and
- 5 Genotype-environment interactions

The review of literature for the estimates of these genetic parameters and their components on some quantitative characters in wheat has been summarized in the following pages:

Attempts to partition genetic variance into components, attributable to different types of gene effects were first made by Fisher (1918). He conceived that genotypic variance can be partitioned into three components, namely, (i) additive portion arising due to difference between

homozygotes, (ii) dominance part resulting from intra-allelic interaction and (iii) an epistatic component associated with interaction of non-allelic genes. He also showed for the first time that the epistatic portion of the genotypic variance, could further be partitioned into different components. Fisher, Immer and Tadin (1932) proposed an experimental approach for separating and measuring additive and dominance effects using second and third degree statistics. Wright (1935) gave detailed division and designation of the genotypic variance into additive, dominance and epistatic variances. These methods were further elaborated by Mather (1949). He developed a method to analyse the quantitative data obtained from non-segregating and segregating generations of a cross between two homozygous parents. The method is based on the partitioning of second degree statistics such as variances and covariances. This methodology partitioned the phenotypic variance of a character and allowed the estimation of the additive genetic variance (D), dominance variance (H) and environmental components of variance (E_1 and E_2).

The literature on the partitioning of variance due to the interaction of non-allelic genes was non-existent until Cockerham (1954) and Kempthorne (1954) developed methods for further partitioning it into two- and higher-order interactions, viz. additive x additive, additive x dominance, dominance x dominance and higher order non-allelic interaction variances. The presence of epistatic effects was further realized by

Anderson and Kempthorne (1954) in red pepper and Hayman (1954, 1957) in Nicotiana and maize respectively. Hayman and Mather (1955) and Hayman (1958) developed statistical techniques for the separation of epistatic effects from the other types of gene effects.

Most genetic models, particularly those for second degree statistics, which have been developed to estimate the components of continuous variation, have as one of their simplifying assumptions, the absence of epistasis. This assumption may hold good for some characters in certain populations only. Very few analyses, however, provide a valid test for the detection of epistasis. A design which is a simple extension of the design III of Comstock and Robinson (1952) has been developed by Kearsey and Jinks (1968) and is called as triple test-cross. It provides not only a precise test for epistasis but also gives unbiased estimates of additive (D) and dominance (H) components, if epistasis is absent. Further this approach is independent of both the gene frequencies and the mating system of the population to be investigated.

A compendium of the review of literature on the following characters/aspects is given :

1 Maturity characters

- a Days to flower
- b Days to maturity

: 8 :

2 Plant/development characters

- a Early vigour
- b Plant height
- c Number of tillers
- d Harvest index

3 Yield and yield components

- a Yield per plant
- b Length of spike
- c Number of spikelets per spike
- d Number of grains per spike
- e 100-kernel weight

4 Protein content

5 Genotype-environment interaction, and

6 Genetic analysis through triple test-cross

2.1 Maturity characters

- a Days to heading
- b Days to maturity

It has been shown by many workers that days to heading in wheat is an additively inherited character (Crumacker and Allard, 1962; Chapman, 1967; Johnson et al., 1966; Bhatt, 1972). Kandola and Anand (1974) evaluated a population of 20 pure lines of wheat using two lines with phenotypic extreme as testers and reported the presence of both additive and non-additive types of variances for days to 50 per cent heading with the additive variance having higher magnitude. Ketata,

Edwards and Smith (1976 b) also reported non-additive gene action for days to heading but the magnitude was biased because of duplicate epistasis. Ali and El-Haddad (1978) and Kassem (1978) also reported additive gene effects with partial dominance in F_2 and F_1 to F_3 generations, respectively for this trait. Sharma et al. (1978) while working on F_1 and F_2 progenies generated through diallel cross mating in wheat observed both additive and dominance gene actions in both the generations for days to heading and days to maturity, except for days to maturity in F_2 , where only additive gene action was recorded. They further reported the preponderance of dominance for days to heading and of additive genetic variance for days to maturity in both the generations.

Sayed (1978) studied a diallel set of six wheat cultivars and observed additive variance for days to heading. Singh and Dwivedi (1978) also reported additive variance for this trait, while Quick (1978) pointed out the presence of both additive and non-additive gene actions for this character. Gupta and Ahmad (1979) studied genetic parameters on macroni wheat in F_1 and F_2 generations and found that additive and non-additive types of gene actions were present for both the characters in both the populations with partial dominance in F_1 and overdominance in F_2 generation.

2.2 Plant/developmental characters

- a Early vigour
- b Plant height
- c Number of tillers
- d Harvest index

The results of various investigations have revealed varied reports regarding the inheritance of plant/developmental traits in wheat. Selim (1960) and Allen and Vogel (1963) reported partial dominance of tallness over shortness. Additive type of gene action for plant height was reported by Powell and Schlehuger (1967). Johnson et al. (1966) reported additive gene effects for plant height while Mahal (1972), Gill et al. (1973) and Kandola and Anand (1974) revealed the presence of both additive and non-additive gene effects for plant height. Chapman and McNeal (1971) observed highly significant epistatic effects for plant height and number of heads in the first year and non-significant epistatic effects for the same traits in the second year.

Aulakh et al. (1973) reported significant predominance of additive variance for number of ears per plant. The gene action governing the expression of harvest index was largely additive both in F_1 and F_2 generations of eight wheat crosses (Bhatt, 1976). However, some of the crosses also exhibited non-additive gene action for this trait. Ketata et al. (1976^b) and Singh and Singh (1978) reported the existence of significant epistasis for plant height and tiller number.

Gill et al. (1977) studied two spring x winter wheat crosses and observed the presence of complete to over-dominance for plant height and tiller number. They further indicated that for tiller number the pattern of inheritance was additive, whereas for plant height additive, dominance and epistatic gene effects were important. Sayed (1978) in a diallel set among six cultivars observed additive variance for plant height while both additive and non-additive variances were detected for number of spikes per plant. Ali and El-Haddad (1978) reported over-dominance for harvest index and partial dominance for plant height and number of tillers per plant in the F_2 families of a 5 x 5 diallel in spring wheat. Balalic and Borojevic (1978) and Singh (1978) reported both additive and non-additive components for number of tillers.

Sharma et al. (1978) conducted combining ability analysis in a diallel cross consisting of ten diverse lines of wheat in F_1 and F_2 and found significant additive and non-additive variances for early growth vigour, plant height and productive tillers in both the generations. They further reported that the magnitudes of additive gene action were lower than those of non-additive gene action for early vigour and productive tillers in F_1 and F_2 and for plant height in F_2 only, thus reflecting the preponderance of non-additive genetic component for these traits. Quick (1978) also observed the presence of additive and non-additive gene actions for plant

height and tiller number in a combining ability analysis on durum wheats.

Singh and Dwivedi (1978) estimated genetic parameters through bi-parental matings in wheat and reported that the plant height was governed by additive genetic variance while both additive and dominance variances were prominent for tillers per plant. Gill, Bhullar and Mahal (1979 a) conducted studies for the estimation of gene action in seven-parent diallel cross of macroni wheat and reported partial dominance for plant height with high heritability.

Gupta and Ahmad (1979) evaluated F_1 and F_2 families in macroni wheat through a line x tester analysis for a number of traits. They observed that both additive genetic variance and dominance variance were significant for plant height, number of productive tillers, harvest index and early vigour in both the generations. Plant height and number of productive tillers showed partial dominance in F_1 generation and overdominance in F_2 generation, whereas early vigour displayed consistent over-dominance. Complete dominance was observed for harvest index in F_1 and overdominance in F_2 .

2.3 Yield and yield components

- a Yield per plant
- b Length of spike
- c Number of spikelets per spike
- d Number of grains per spike
- e 100-kernel weight

Grain yield in wheat was reported to be polygenic character as early as 1935 by Aamodt, Torrie and Wilson. Since then various workers have reported existence of dominance, partial dominance, complete dominance and overdominance relationships for grain yield and its components in wheat. Overdominance for grain yield was reported by Schmidt and Johnson (1962), Patterson and Bitzer (1966) and Gyawali et al. (1968). From the study of a cross of wheat, Mahal (1972) and Gill et al. (1973) also reported additive gene effects for spike length, number of grains per spike and grain yield per plant, while dominance gene effects were stated to be responsible for the expression of grain weight. Chapman and McNeal (1971) demonstrated the existence of additive gene effects for number of spikelets per spike; both additive and dominance types of gene actions for kernel weight and highly significant epistatic effects for grain yield through generation means analysis. The epistatic effects for grain yield were found to be absent in the next year.

Aulakh et al. (1973) investigated a population of bread wheat in F_2 generation and revealed that both additive and non-additive variances were significant for grain yield, spikelet number and 100-grain weight while only additive variance was significant for number of grains per ear. They further stated that the magnitudes of additive variance were much higher than those of non-additive variances for these traits.

Virk and Verma (1973) compared different biometrical procedures for the study of gene action in barley. They advocated that the methodology of Jinks et al. (1959) appeared to be the most efficient for the detection of epistasis, because the level of epistasis detected in this material could not be indicated by W_r/V_r graph. Grain yield was influenced by epistasis and with the exclusion of interacting parent, although the epistasis vanished but the magnitudes of sums and differences remained almost unaltered under both the situations and were highly significant with the absence of directional dominance in overdominance range. Ketata et al. (1976 b) revealed that no epistasis could be detected for spikelets per spike, kernels per spike and kernel weight indicating that estimates of gene effects for these characters were free from linkage bias. However, significant epistasis was observed for grain yield.

Gill et al. (1977) studied two spring x winter wheat crosses and observed partial to complete dominance for ear length and number of spikelets. They further stated that the pattern of inheritance for ear length was additive, whereas, for number of spikelets per spike additive, dominance and epistatic gene effects were important.

Singh and Singh (1978 a) also observed epistasis (dominance x dominance) as a major component controlling the expression of grain yield, number of spikelets per spike and

length of spike in some crosses of wheat. Simple additive-dominance model was found to be adequate for length of spike and number of spikelets per spike in one cross.

Sharma et al. (1978) conducted combining ability analysis in a diallel cross consisting of ten diverse lines of wheat in F_1 and F_2 generations and found significant additive and non-additive variances for grain yield per plant, spikelets per spike, grains per spike and 100-kernel weight in the two generations. The magnitudes of additive component were lower than those of non-additive component and thus reflected the preponderance of non-additive genetic component for these traits. Singh (1978) reported additive component of genetic variance for grain yield per plant, spike length and 100-grain weight, whereas additive and dominance components of genetic variance for number of grains per spike. Sayed (1978) observed additive genes for number of spikelets per spike and kernels per spike, both additive and non-additive genes for 1000-grain weight and mainly non-additive genes for grain yield in a study of a diallel set involving six cultivars of wheat. Tsil'ke et al. (1978) also reported additive gene action for number of spikelets per ear. Singh and Dwivedi (1978) estimated genetic parameters through bi-parental mating in wheat and demonstrated that the estimates of additive genetic components were predominant for spike length, grains per spike and yield per plant, whereas additive and non-additive genetic components were significant for test weight.

Schmidt et al. (1978) grew a diallel set of eight parents to study genetic parameters for yield and yield components and found significant GCA effects for yield, spikes per plant and kernels per spike and both GCA and SCA effects for 1,000-grain weight. Quick (1978) also reported the existence of significant GCA effects for yield and yield components in durum wheats. Gill et al. (1979 a) demonstrated the presence of additive effects for number of grains per ear and of additive, dominance and epistatic effects for grain size and grain yield through generation means analysis. They (1979 b) further reported overdominance for grain yield and grain weight and partial dominance for spike length.

Gupta and Ahmad (1979) evaluated F_1 and F_2 families in macroni wheat through a line x tester analysis for a number of traits. They observed that both additive, genetic and dominance variances were significant for grain yield and yield components in these two generations. Most of the traits in F_2 exhibited the preponderance of non-additive gene action. Yield and its contributing characters reflected overdominance of consistent nature for F_1 and F_2 generations except number of spikelets per main spike which indicated consistent partial dominance in both the generations.

2.4 Protein content

The literature on the type of gene action governing protein content in wheat shows varying reports from different materials (Tandon, 1967; Chapman and McNeal, 1970). Complex genetic control of protein content was reported by Aamodt and Torrie (1935), Kuspira and Unrau (1957) and Stuber et al. (1962). Chapman and McNeal (1970) observed the absence of epistasis for protein content in all the crosses studied by them. Rao and Murty (1970) found non-additive gene action for protein content in wheat.

Singh et al. (1978) reported studies relating to the genetic parameters for protein content and noted additive and non-additive types of gene action for the inheritance of grain protein. Kassem (1978) also reported the presence of additive and non-additive gene actions with overdominance for protein content in wheat grains. Guthrie and Smith (1978) indicated additive genetic effects for this character.

Bhullar et al. (1973) reported that the additive type of gene action was predominant in the inheritance of grain protein, besides dominance, linkage and epistasis of the duplicate type. Arora and Chandra (1980) pointed out that the gene action for protein content was primarily non-additive.

2.5 Genotype-environment interactions

The environment plays an important role in the final phenotypic expression of a character. A genotype is known to show a differential phenotypic response in development when introduced to different environments. This interplay in effect of genetic and non-genetic forces on development is known as genotype-environment ($G \times E$) interaction. Genotype-environment interactions which commonly occur in plant material, are of considerable significance in a breeding programme. These interactions create manifold difficulties in interpreting results from the experiments carried out in different environments and often hamper the rationalization of policy and procedure in breeding programmes aiming at further genetic improvement in crop plants. In order to remove bias in the estimates of genetic parameters resulting from $G \times E$ interaction, it is necessary that experimental material is tested over a spectrum of environments of interest to the breeder.

Gardener (1963) emphasized the need to determine the relative magnitude of the variances due to the interactions of additive and non-additive gene effects with the environment for making it possible to decide which component of genetic variation could be exploited in a breeding programme. Kronstad and Foote (1964) also emphasized the importance of studies on genotype-environment interactions.

Paroda and Joshi (1970) studied a diallel set of crosses of bread wheat in F_1 , F_2 and F_3 generations during two seasons and observed that variances due to general combining ability interacted more with the environment than those of the specific combining ability for grain yield. A similar picture was depicted for all the characters studied, irrespective of their magnitude.

Bhullar et al. (1975) while studying the estimates of genetic variance in a diallel cross involving seven diverse wheat varieties over generations F_1 to F_5 under three environments indicated that general as well as specific combining ability variances were significant in all the generations and the magnitudes of GCA variances were more than those of SCA variances. They further reported the existence of significant general and specific combining ability x location interactions.

Chaudhary et al. (1978) studied genotype x environment interactions and the genetic architecture of harvest index in wheat. Components of genetic variance interacted with environment to a large extent and it was governed by additive, dominance and epistatic gene effects. Jain and Singh (1978) emphasized the need to determine the relative magnitude of epistatic variance particularly additive by additive type for yield and its components. They studied F_2 and F_3 progenies of three testers and 21 lines of spring wheat generated through Design II

in two environments. The pooled analysis of combining ability over the two generations showed that both SCA and SCA x generation interaction variance components were significant and were of higher magnitude for grain yield and ear number in the two environments. The estimates of genetic variance components defined for F_1 (non-inbred) generation, showed that additive by additive type of epistatic variance had a greater influence on variation in grain yield and ear number. For grain number per ear additive variance was significant but dominance variance component was important in both the environments. For 1,000 grain weight additive variance was important under unirrigated conditions, whereas additive and additive by additive type epistatic variances assumed significance under irrigated conditions. They emphasized that models neglecting epistasis might lead to biased estimates of genetic variances.

Gamzikova et al. (1979) found protein content to be controlled mainly by additive component but some dominance and over-dominance effects were also observed. The expression of genes controlling protein content was greatly modified by environmental conditions. Tsil'ke et al. (1979 a,b) reported that ear length and number of grains per ear were controlled both by additive and dominant genes. A considerable genotype x environment interaction existed for ear length with variable interaction for additive and non-additive gene effects. The

additive effect was stable from year to year for number of grains per ear at low stand, its estimate was larger under high density environment.

Dragavtsev and Aver-Yanova (1979) in a diallel analysis of yield components in 15 varieties grown in eight environments showed that the length of the main stem and ear length having a high degree of additive variance reacted in a similar way under different ecological conditions, while characters grain weight per plant (showing overdominance) and number of grains per spike (showing complementary epistasis) reacted in different ways.

2.6 Genetic analysis through triple test-cross

The triple test-cross breeding programme is an efficient method of detecting and partitioning an epistatic component of variation within a population and for estimating the additive and dominance components in the absence of epistasis. It is an extension of the NCM III design of Comstock and Robinson (1952) and proposed by Kearsey and Jinks (1968). It can be applied to any population regardless of its gene and genotypic frequencies or its degree of inbreeding (Jinks et al., 1969; Perkins and Jinks, 1970; Jinks and Perkins, 1970). The crossing programme is relatively demanding and it could be particularly laborious when the material under investigation produces only one or few

seeds per pollination. This could restrict the experimental size and, therefore, decrease the reliability of the results. In such circumstances, Kearsey and Jinks (1968) suggested using progeny families produced by self-pollinating the individual crosses instead of the crosses themselves.

Furthermore, this approach is best among the available, for the detection of genotype x environment interaction components both with macro- and micro-environments (Perkins and Jinks, 1971; Pooni, Jinks and Jayasekara, 1978). The approach has been simplified and modified in a number of ways for the restricted case of populations of inbred lines (Jinks et al., 1969; Virk and Jinks, 1977; Jinks and Virk, 1977). The review of work done through this approach on wheat is summarised here :

Ketata, et al. (1976 a) studied the genetical components of variation in winter wheat crosses involving the triple test-cross breeding design. The results of two experiments involving different materials were generally consistent with respect to the detection of epistasis. They demonstrated that non-allelic interactions affected the expression of heading date, kernels per spikelet and grain yield, but these did not affect the expression of plant height, protein content, tiller number, spikelets per spike and kernels per spike in both the experiments. Epistasis was indicated for kernel weight in one experiment but not in the other.

Additive gene action was predominant in both experiments for protein content, spikelets per spike and kernels per spike. Evidence for dominance was obtained for plant height and kernels per spike in one experiment. It was suggested that epistasis might be non-trivial factor in the inheritance of agronomic traits in this material and genetic models neglecting epistasis might result in biased information.

Singh and Singh (1976) applied the modified triple test-cross to the study of additive, dominance and epistatic components of genetic variance for five metric traits, namely, final plant height, ear length, number of spikelets per spike, number of grains per spike and grain yield per plant in two wheat crosses (Kalyan Sona x Norteno 67 and Norteno 67 x WL 212). The results of the analysis revealed that the epistatic component of genetic variation was an important element in both the crosses for all the five characters. Further partitioning of the epistasis item, however, revealed that epistasis (i) type was not significant for spikelets per spike in the first triple test-cross and for final plant height, ear length and spikelets per spike in the second. It was further observed that the items due to sums and differences were significant in both the crosses for all the characters studied. Accordingly, the components D and H were significant for all the traits in both the sets. However, these estimates of D and H were biased by epistasis to an unknown extent and the unbiased estimates were

not computed. The relative magnitudes of additive and dominance variances differed with the material involved. Thus in one of the crosses, the additive variance was more, whereas, for the other, the dominance was, in general, of higher magnitude for most of the traits studied.

Singh and Singh (1978 b) studied the first back-cross populations of four wheat crosses through triple test-cross analysis for detecting and estimating the additive, dominance and epistatic components of genetic variation for four metric traits, namely, final plant height, number of spikelets per spike, 100-kernel weight and yield per plant, Epistasis was more important component of variation for final plant height and yield per plant than for number of spikelets per spike and 100-grain weight. On the other hand, the additive component was highly significant for all the four characters in all eight back-crosses.

Singh (1979) compared three analyses namely, design I and II of Comstock and Robinson and Standard design III of Kearsey and Jinks in respect of gene action for plant height, spikelet number per spike and yield per plant in the F_2 's of the three crosses. The three analyses agreed closely with regard to estimates of the additive component for all the three characters in all the three crosses. Standard design III was the most efficient for estimating the dominance

component for all the three characters except the number of spikelets per spike in one cross.

Singh (1980 b) reported the results of a triple test-cross breeding programme on wheat using the approach of Kearsey and Jinks (1968), Jinks et al. (1969), Perkins and Jinks (1971), Virk and Jinks (1977) and Jinks and Virk (1977) for five traits, viz. final plant height, spike length, number of spikelets per spike, 100-kernel weight and grain yield per plant over two years. Epistasis was an important element for yield per plant in both the years. Absence of significant epistasis was observed for two component traits of yield, namely, spike length and number of spikelets per spike, in these two years. Further partitioning of $(L_{1i} + L_{2i} - 2L_{3i})$ item showed that wherever epistasis was present (i) type as well as (j and l) type gene effects participated in the control of the characters except for 100-grain weight in the first year, where only (i) type gene effects were important. Dominance was directional in all cases. Additive genes were most sensitive to micro- as well as to macro-environmental differences, whereas the dominance component showed least sensitivity to macro-environmental differences. He further reported the existence of (i) epistasis x environments interaction for plant height and yield per plant and (j and l) epistasis x environment interactions for plant height and 100-kernel weight.

Study of the genetic parameters is the basic step for any planned breeding project towards increasing productivity. Very limited systematic work has been done so far in wheat utilizing triple test-cross mating design. This design is the best among the various other mating designs, available, both for the study of genetical architecture and G x E interaction components of randomly breeding populations. The estimates of additive and dominance components of genetic variation obtained from the triple test-cross analysis are uncorrelated and have identical sampling errors and thus provide an unique opportunity to compare the relative sensitivity of the different kinds of gene actions (additive, dominance and epistasis) to the environmental differences. This advantage of TTC has yet to receive the attention of wheat breeders, particularly for the efficient detection of epistasis.

There are a few reports on genetic parameters for yield and its associated primary and secondary traits using this design, whereas information of similar nature is scanty on selfs from TTC. Since, some physical and genetic barriers limit the value of F_1 materials to some extent, it may be worthwhile to obtain the precise values of genetic parameters in F_2 or advanced generations. In the present investigation these aspects have been studied in spring wheat.

Chapter III

MATERIAL AND METHODS

The present investigation was carried out during the years 1976-77 to 1978-79 at the Satyanand Stokes Horticultural Complex, Solan, Himachal Pradesh Krishi Vishva Vidyalaya, Palampur.

3.1 Material

The experimental material consisted of a random sample of ten pure breeding lines of spring wheat and two agronomically superior and genetically diverse pure lines maintained in the Department of Plant Breeding and Genetics. Thus 12 genotypes were included in the present study. Of these, WG 377 and HS 13 were used as L_1 and L_2 testers and the F_1 between them (WG 377 x HS 13) as L_3 tester. WG 377 and HS 13 were chosen as testers because among the 12 varieties included in the study, these were extreme phenotypes for plant height, 100-kernel weight and grain yield. The salient features of these 12 genotypes are summarized below :

<u>Sr. No.</u>	<u>Genotype and pedigree</u>	<u>Principal characteristics</u>
<u>Testers</u>		
1	WG 377 (WG 143 x USA 255) x PV 18	A single-dwarf wheat with good tillering capacity and yield. Grains of medium size, hard, lustrous and amber. Medium maturity with weak straw
2	HS 13 (E 4878 x S 308)	A double-dwarf variety with good tillering and stiff straw. Grains of bold size, medium soft and amber. Early maturity, susceptible to leaf rusts
<u>P_i lines</u>		
1	Cno x Nar-chris/Tob- 8156-Ceno	A double-dwarf wheat with good tillering capacity and yield. Bold, hard and amber grains, early maturity
2	Cno-Bb x Cal (7C/Lib.- Inia x Inia Bb)	A double-dwarf strain. Grains of bold size, hard and red. Highly resistant to rusts
3	K 4328 (D1A)	A variety of Ethiopian origin. Medium tall, good tillering, medium soft grains. Most resistant to <u>S. tritici</u> , <u>S. nodorum</u> and <u>Septoria</u> spp.
4	Inia 'S'-7C	Mid-November planting, resistant to rusts, strong straw, red grains
5	L 193	A variety from Lebanon. Late maturity. Grains red, hard and small
6	Ceno-chris	A medium tall strain with good tillering, early maturity and red, hard grains. It has field resistance to yellow and brown rusts

Sr. No.	Genotype and pedigree	Principal characteristics
7	Cno 'S'- cBo215	A double dwarf strain with good tillering, medium maturity and high yield. Light soft red grains
8	Cno "S"-Inia'S'	A double-dwarf strain, medium maturity with optimum sowing date mid-November. High resistance to rusts. Red grains
9	No.66-Cno'S'	Medium tall wheat, early maturity, good tillering, medium bold red grains. Resistant to most stem and leaf rust races
10	Cno-cPo x S2	A short statured, medium maturity wheat with light soft amber grains

3.2 Methods

3.2.1 Crossing plan

The crosses were developed according to the mating design proposed by Kearsey and Jinks (1968). In the first year WG 377 was crossed to HS 13 and sufficient F_1 seed produced. During the second year the above mentioned 10 P_i lines were crossed to three female testers, viz. WG 377 (L_1), HS 13 (L_2) and the F_1 of WG 377 and HS 13 (L_3). The crossing plan thus yielded 3n progenies comprising 30 crosses, in a triple test-cross design.

: 30 :

3.2.2 Design and layout

The 30 families (L_{1i} , L_{2i} and L_{3i}) alongwith the two testers were grown in a randomized complete-block design with three replications in 1977-78 and the selfs of these 30 families, two testers and ten P_i lines were grown during 1978-79. These materials were grown on two different sowing dates, i.e. one at normal sowing time (15th November) and the other three weeks late (6th December) than the usual sowing time to provide for two different environments in the year 1978-79. The details of the layout are given below

Year	Experiment	Material	No. of rows	Row length	Spacing	
					Row to row	Plant to plant
1977-78	I	30 families of TTC plus two testers	1	1.5 m	30 cm	10 cm
1978-79	II and III	Selfs of 30 TTC families plus 2 testers plus 10 P_i lines	3	4.0 m	30 cm	5 cm

3.2.3 Recording of observations

The observations were recorded in each replication on the following characters :

Early yield

Early vigour

All the plants in a plot were scored for early vigour keeping in view the vegetative growth, number of leaves and height at seedling stage. The scoring was on the basis of one good to nine poor.

Days to heading

Number of days from sowing, to the date when 50 per cent of the spikes from the main shoot in a plot had completely emerged, was recorded.

Days to maturity

Number of days taken from sowing to the date when 80 per cent of the spikes had reached the physiological maturity, were recorded.

Plant height

Final height of the main shoot was measured in centimetres at the time of harvest on ten randomly selected plants from ground level to the tip of spike on the main shoot, excluding awns.

Number of tillers per plant

Number of effective tillers at the time of maturity on ten randomly chosen plants was counted and averaged.

Harvest index

All the ten plants marked for recording observations were harvested at the ground level and total biological weight recorded. All the spikes from these plants were threshed. The harvest index was then computed as the ratio of the yield of grains to the biological yield.

Spike length

Length of spike in centimetres excluding awns was recorded on ten random spikes in each entry.

Number of spikelets per spike

Observation on number of spikelets per spike was recorded on ten random spikes taken for spike length.

Number of grains per spike

Observations on number of grains were taken on five spikes threshed in bulk and the number of kernels per spike computed on the mean basis.

Kernel weight

100-kernels were counted from the bulked yield of ten plants of each family and weight was recorded in grams.

Grain yield per plant

All spikes of the ten plants were threshed together to record yield in grams and the mean yield per plant was computed.

Protein content

100-grains used for recording kernel weight were ground to determine protein content through Lowry method (Lowry et al., 1951).

Lowry method of protein assay

Principle

Protein reacts with the Folin-Ciocalteu reagent to give a coloured complex. The colour so formed is due to the reaction of the alkaline copper with the protein as in the biuret test and the reduction of phosphomolybdate by tyrosine and tryptophan present in the protein.

Material

- 1 Alkaline sodium carbonate solution (2% Na_2CO_3 in 0.1N NaOH)
- 2 Copper sulphate-sodium potassium tartrate solution (0.5% CuSO_4 in 1% Na, K tartrate). Prepared fresh by mixing stock solutions
- 3 'Alkaline solution' was prepared on day of use by mixing 5 ml of (1) and 1 ml of (2)
- 4 Folin-Ciocalteu reagent. (Diluted the commercial reagent with an equal volume of water on the day of use. This is a solution of sodium tungstate and sodium molybdate in phosphoric hydrochloric acid)
- 5 Standard protein (albumin solution 0.2 mg/ml)

Method

Five ml of the alkaline solution was added to 1 ml of the test solution. Thoroughly mixed and allowed to stand at room

temperature for 10 minutes or longer. 0.5 ml of diluted Folin-Ciocalteu reagent was rapidly added with immediate mixing. After 30 minutes the extinction against the appropriate blank at 750 nm was read.

Estimated the protein concentration of an unknown solution after preparing a standard curve.

3.2.4 Statistical Procedures

Randomized complete-block design was used for conducting the present studies. The model for this design is as under :

Population model for a randomized complete-block experiment

Observation = Overall mean + Block effect + Treatment + Error effect

$$Y_{ij} = \mu + \alpha_i + \beta_j + e_{ij}$$

$$i = 1, \dots, r, \quad j = 1, \dots, g$$

Where the parameters satisfy

$\sum \alpha_i = 0$, $\sum \beta_j = 0$, and the e_{ij} 's are random errors independently distributed as $N(0, \sigma^2)$.

Analysis of variance of this design for every character is presented in the form of table as :

Analysis of variance of different progenies		
Source of variation	d.f.	Expectation of M.S.
Replicates	(r-1)	$\sigma^2 + r\sigma_g^2$
Progenies	(g-1)	$\sigma^2 + r\sigma_g^2$
Error	(r-1)(g-1)	σ^2
Total	rg-1	

3.2.4.1 Genetic Analysis

The information on the genetic architecture of the material under investigation was gathered through triple test-cross design. The analysis of triple test-cross design is divided into two parts : (i) the test for epistasis and the adequacy of the model, and (ii) the estimation of the additive and dominance components of variation if epistasis is absent.

Tests for epistasis and adequacy of testers

In a full triple test-cross of a population of pure breeding lines, two separate tests for the simple model, which when applied simultaneously can determine the presence of non-allelic interactions and the inadequacy of the testers (Jinks and Virk, 1977). These two tests are based upon the following comparisons :

Test	Comparison	Reference
I $\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$	1 1 -2	Kearsey and Jinks, 1968
II $\bar{L}_{1i} + \bar{L}_{2i} - \bar{P}_i$	1 1 -1	Jinks, Perkins and Breese, 1969

The test $\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$ is unambiguous and always tests the presence of epistasis for non-common loci between the L_1 and L_2 testers.

An analysis of variance for the P_i families ($i = 1$ to n) was performed with the following partitioning :

Analysis of variance to test for epistasis and its components	
Item	d.f.
Epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$)	n
(a) Epistasis ($\underline{i}$) type	1
(b) Epistasis ($\underline{j}$ and $\underline{l}$) type	$n-1$
Replicates x Epistasis	$n (r-1)$
(a) Replicates x Epistasis ($\underline{i}$)	$(r-1)$
(b) Replicates x Epistasis ($\underline{j}$ and $\underline{l}$)	$(r-1)(n-1)$
Within families error	$3nr (m-1)$

The epistasis sum of square for n d.f. was further partitioned into an item, testing ($\underline{i}$) type epistasis (homozygote x homozygote interaction) and an item testing ($\underline{j}$ and $\underline{l}$) type of epistasis, the homozygote x heterozygote and heterozygote x heterozygote interactions respectively. Similarly, the sum of squares due to replicates x epistasis for $n(r-1)$ degrees of freedom was sub-divided into two items, namely, replicates x epistasis ($\underline{i}$) type and replicates x epistasis ($\underline{j}$ and $\underline{l}$) type with $(r-1)$ and $(r-1)(n-1)$ degrees of freedom respectively.

The test $\bar{L}_{1i} + \bar{L}_{2i} - \bar{P}_i$ provided the second test of the simple model. The analysis of variance for testing the

significance of $V(\bar{L}_{1i} + \bar{L}_{2i} - \bar{P}_i)$ quantities over $i = 1$ to n lines was tested as suggested by Jinks et al. (1969) and has the following form :

Analysis of variance to test for epistasis		
Item	d.f.	Expectation of M.S.
Replicates	$(r-1)$	
Epistasis $(\bar{L}_{1i} + \bar{L}_{2i} - \bar{P}_i)$	$(n-1)$	$\frac{1}{m} \bar{\sigma}_w^2 + \bar{\sigma}_r^2 \times \text{epist} + 3\bar{\sigma}_{\text{epi}}^2$
Replicates x Epistasis	$(r-1)(n-1)$	$\frac{1}{m} \bar{\sigma}_w^2 + \bar{\sigma}_r^2 \times \text{epi}$
Within families error	$3nr(m-1)$	$\frac{1}{m} \bar{\sigma}_w^2$

On the basis of tests I and II applied for the detection of epistasis, the following four situations can arise each of which has its own interpretation.

a Neither test I nor test II is significant

This means that there is no detectable epistasis and the testers are adequate. Alternatively the testers may be inadequate but there is no dominance and hence the estimate of the additive genetic component is unbiased.

b Test I is non-significant and test II is significant

This indicates that there is no epistasis but the testers are inadequate because they share common alleles.

c Test I is significant and test II is non-significant

This is trivial in that it could only arise if the two tests differ in their sensitivities to epistasis.

d Both tests I and II are significant

This indicates that epistasis is present but we can not be sure of the adequacy or inadequacy of the testers. Any estimate of the genetical parameters will thus be biased by either non-allelic interactions or possibly by inadequate testers.

Estimation of additive and dominance components of variation

The analysis of additive and dominance effects is exactly as described by Comstock and Robinson (1952), i.e. by obtaining the variances of sums and differences of $\bar{L}_{1i}$ and $\bar{L}_{2i}$, except that $\bar{6}^2$ ml has been re-defined and is equal to $\frac{1}{2} \bar{6}^2$ ml of Comstock and Robinson. This change was made simply to facilitate comparisons between additive and dominance components.

The additive (D) and dominance (H) components of genetic variation can be estimated from the following orthogonal comparisons :

Comparison	L_{1i}	L_{2i}	L_{3i}	Component
Sums	1	1	0	Additive (Kearsey and Jinks, 1968)
Differences	1	-1	0	Dominance (Kearsey and Jinks, 1968)

and the test of significance was applied by setting up the following analysis of variance :

Analysis of variance of sums and differences

Item	d.f.	M.S.	Expectation of M.S.
<u>Analysis of sums</u>			
Replicates	(r-1)	M_{11}	
Sums ($\bar{L}_{1i} + \bar{L}_{2i}$)	(n-1)	M_{12}	$\frac{1}{m} \sigma_w^2 + \sigma_{nr}^2 + 2r\sigma_m^2$
Sums x Replicates	(n-1)(r-1)	M_{13}	$\frac{1}{m} \sigma_w^2 + \sigma_{nr}^2$
Within families error	2nr(m-1)	M_{14}	$\frac{1}{m} \sigma_w^2$
<u>Analysis of differences</u>			
Replicates	(r-1)	M_{21}	
Differences ($\bar{L}_{1i} - \bar{L}_{2i}$)	(n-1)	M_{22}	$\frac{1}{m} \sigma_w^2 + \sigma_{nr}^2 + 2r\sigma_{ml}^2$
Differences x Replicates	(n-1)(r-1)	M_{23}	$\frac{1}{m} \sigma_w^2 + \sigma_{nr}^2$
Within families error	2nr(m-1)	M_{24}	$\frac{1}{m} \sigma_w^2$

On a simple additive-dominance model the additive and dominance components of variation were estimated as :

$$D = 4 \sum \bar{u} \bar{v} d_i^2 = 4 \sigma_m^2$$

$$H_1 = 4 \sum \bar{u} \bar{v} h_i^2 = 4 \sigma_{ml}^2$$

For the selfed progenies the components of genetic variation were computed as :

$$\begin{aligned} D &= 4 \overline{6m}^2 \\ H_1 &= 16 \overline{6ml}^2 \text{ and} \\ (H_1/D)^{\frac{1}{2}} &= \text{average degree of dominance} \end{aligned}$$

The covariance of $\bar{L}_{1i} + \bar{L}_{2i}$ on $\bar{L}_{1i} - \bar{L}_{2i}$ for all values of i was calculated as described by Jinks et al. (1969). The covariance was then converted into 'F' which in the absence of epistasis and correlated gene distribution has the expectation $-\frac{1}{4} F = \text{Cov. sums/differences} = -\sum_j uvd_j \quad h_j$ for the normal triple test-cross and $-\frac{1}{8} F$ for selfs of triple test-cross. $-F$, therefore, has the same coefficient as D and H for normal triple test-cross and it reduces by one half for each selfing generation. It measures the sum of the products of the d and h terms. Both the magnitude and the sign of the covariance provide information about the magnitude and direction of dominance obtained from $\overline{6m}^2$. The significance of covariance was tested by converting it into a correlation coefficient with $(n-3)$ degrees of freedom.

$$r_{\text{sums/differences}} = \frac{\text{Cov}_{\text{sums/differences}}}{\sqrt{V_{\text{sums}} \times V_{\text{differences}}}}$$

A number of situations can occur in practice for each of which has its own interpretation. These are :

a $\hat{G}_{ml}^2$ is significant and $r_{\text{sums/differences}}$ is significant

It indicates the presence of dominance variation and that is predominantly in one direction. F which has the opposite sign of the covariance, if positive, indicates the dominance of increasing alleles and if negative, the (vice-versa) decreasing alleles are dominant.

b $\hat{G}_{ml}^2$ is significant and $r_{\text{sum/differences}}$ non-significant

This means that there is a dominance contribution to the variation but the dominance is ambidirectional, increasing and decreasing alleles being dominant and recessive to the same extent.

c $\hat{G}_{ml}^2$ is non-significant and $r_{\text{sum/difference}}$ is non-significant

This shows that there is no evidence of dominance contribution to the variation.

d $\hat{G}_{ml}^2$ is non-significant and $r_{\text{sum/difference}}$ is significant

This is trivial and could only arise as a result of sampling error.

Estimation of unbiased components

If the simple model fails due to the presence of common loci in the testers we can still estimate unbiased genetical components. In this situation the test $\bar{L}_{1i} + \bar{L}_{2i} - \bar{P}_i$ will

be significant, whereas the test $\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$ will be non-significant. This type of situation indicates the absence of non-allelic interactions and the inadequacy of testers.

The estimation of unbiased components in these situations was done as suggested by Jinks and Virk (1977) and Virk and Jinks (1977) and using their notations on a simple model we can make the following orthogonal comparisons :

Comparison	$\bar{L}_{1i}$	$\bar{L}_{2i}$	$\bar{L}_{3i}$	$\bar{P}_i$	Component
1	1	1	1	0	σ_s^2
2	1	-1	0	0	σ_d^2
3	0	0	0	1	σ_p^2

The first comparison replaces the variance of $\bar{L}_{1i} + \bar{L}_{2i}$ as suggested by Jinks and Perkins (1970) for estimating σ_s^2 while comparison 2 is that originally suggested by Kearsey and Jinks (1968) for computing σ_d^2 . The third comparison which estimates σ_p^2 will always give unbiased estimates of additive genetic component (D), since it is independent of the testers used. The genetical expectations of the components of variance obtainable from these comparisons would therefore, be :

$$\begin{aligned} \sigma_s^2 &= \frac{1}{4} D_k + \frac{1}{4} H_{k_1} - \frac{1}{2} F_{k_1} \\ \sigma_d^2 &= \frac{1}{4} H_{k_2} \end{aligned}$$

: 43 :

$$\sigma_p^2 = D_k$$

$$\sigma^2(\bar{L}_{1i} + \bar{L}_{2i} - \bar{P}_i) = 1/9 H_k$$

$$\text{Cov}(\bar{L}_{1i} + \bar{L}_{2i})(\bar{L}_{1i} - \bar{L}_{2i}) = -1/4 F_{k_2}$$

where:

$$\sigma_s^2 = \text{Variance due to sums}$$

$$\sigma_d^2 = \text{Variance due to differences}$$

$$\sigma_p^2 = \text{Variance due to parental lines}$$

$$\sigma^2(\bar{L}_{1i} + \bar{L}_{2i} - \bar{P}_i) = \text{Variance due to common loci}$$

$$\text{Cov}(\bar{L}_{1i} + \bar{L}_{2i})(\bar{L}_{1i} - \bar{L}_{2i}) = \text{Variance of sums and differences}$$

k stands for total number of loci of which k_1 are common and k_2 non-common in the two testers.

Now the estimation of unbiased components is :

$$D_k = \sigma_p^2$$

$$H_k = 4 \sigma_d^2 + 9 \sigma^2(\bar{L}_{1i} + \bar{L}_{2i} - \bar{P}_i)$$

$$F_k = \sigma_p^2 + 9 \sigma^2(\bar{L}_{1i} + \bar{L}_{2i} - \bar{P}_i) - 4 \text{Cov sums/diff} - 4 \sigma_s^2$$

The magnitude of H_k and F_k in selfing generations are :

$$H_k = 16 \sigma_d^2 + 9 \sigma^2(\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i)$$

$$F_k = \sigma_p^2 + 9 \sigma^2(\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i) - 8 \text{Cov sum/diff} - 4 \sigma_s^2$$

where, D_k , H_k and F_k are the unbiased additive, dominance and inbreeding coefficients respectively.

Standard error of the estimates

The standard errors for different estimates were computed firstly by obtaining the variance of the related variances by the help of the following formulae (Verma and Gill, 1975) :

$$V_D = \frac{1}{r^2} \left\{ \frac{8 (M_{12})^2}{df} + \frac{8 (M_{13})^2}{df} \right\}$$

$$V_H = \frac{1}{r^2} \left\{ \frac{8 (M_{22})^2}{df} + \frac{8 (M_{23})^2}{df} \right\}$$

and

V_H for selfed progenies as :

$$\frac{1}{r^2} \left\{ \frac{128 (M_{22})^2}{df} + \frac{128 (M_{23})^2}{df} \right\}$$

and the square root of the respective variance gave the appropriate standard error of the estimate.

2.4.2 Genotype x Environment interaction

The interaction between the progeny genotypes of a triple test-cross and the macro-environments of their testing was computed according to the approach outlined by Perkins and Jinks (1971). If r individuals of each of the $\bar{L}_{1i}$, $\bar{L}_{2i}$ and $\bar{L}_{3i}$ progeny families of a triple test-cross, where $i = 1$ to n are raised in each of s environments, the following items from an analysis of variance can be extracted :

Analysis of triple test-cross grown in varying environments

Item	d.f.	
<u>Analysis of epistasis</u>		
Test I ($\bar{L}_{1is} + \bar{L}_{2is} - 2\bar{L}_{3is}$)		
Epistasis (<u>i</u>) type	1	
Epistasis (<u>i</u>) x Environments	(s-1)	
Replicates within environments	s(r-1)	
Epistasis (<u>j</u> and <u>l</u>) type	(n-1)	
Epistasis (<u>j</u> and <u>l</u>) x Environments	(n-1)(s-1)	
Pooled error	s(n-1)(r-1)	
Test II ($\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$)		
Environments	(s-1)	
Replicates within environments	s(r-1)	
Epistasis	(n-1)	
Epistasis x Environments	(n-1)(s-1)	
Pooled error	s(n-1)(r-1)	
<u>Analysis of sums</u>		<u>Expectation of M.S.</u>
Environments	(s-1)	
Replicates within environments	s(r-1)	
Sums ($\bar{L}_{1is} + \bar{L}_{2is}$)	(n-1)	$\bar{\sigma}_1^2 + 2r \bar{\sigma}_{sm}^2 + 2rs \bar{\sigma}_m^2$
Sums x Environments	(n-1)(s-1)	$\bar{\sigma}_1^2 + 2r \bar{\sigma}_{sm}^2$
Pooled error	s(n-1)(r-1)	$\bar{\sigma}_1^2$

Item	d.f.	Expectation of M.S.
<u>Analysis of differences</u>		
Environments	(s-1)	
Replicates within environments	s(r-1)	
Differences ($\bar{L}_{1is} - \bar{L}_{2is}$)	(n-1)	$\sigma_2^2 + 2r \sigma_{sm}^2 + 2rs \sigma_{ml}^2$
Differences x Environments	(n-1)(s-1)	$\sigma_2^2 + 2r \sigma_{s ml}^2$
Pooled error	s(n-1)(r-1)	σ_2^2

The variances in terms of the parameters of the biometrical genetical model extracted from the above analysis of variance under the simplest situation were translated as :

$$\begin{aligned}
 D &= 4 \sigma_m^2 \\
 H &= 16 \sigma_{ml}^2 \\
 G_{2D} &= 4 \sigma_{sm}^2 \\
 G_{2H} &= 16 \sigma_{s ml}^2
 \end{aligned}$$

where :

$$\begin{aligned}
 D &= \text{Additive component of variation} \\
 H &= \text{Dominance component of variation} \\
 G_{2D} &= \text{Macro-environmental additive interaction component} \\
 G_{2H} &= \text{Macro-environmental dominance interaction component}
 \end{aligned}$$

Chapter IV

EXPERIMENTAL RESULTS

The material for the present investigation comprised two agronomically superior and genetically diverse homozygous varieties of spring wheat, namely WG 377 and HS 13 and 10 other pure breeding lines. WG 377 and HS 13 were designated as L_1 and L_2 testers and the F_1 between them (WG 377 x HS 13) as L_3 tester and the pure breeding lines as P_i s. These 10 P_i lines were crossed to each of the L_1 , L_2 and L_3 testers to produce 30 families, i.e. L_{1i} , crosses of L_1 with P_i ; L_{2i} , the crosses of L_2 with P_i and L_{3i} , the crosses of L_3 with P_i , to form a triple test-cross. These 30 triple test-cross progenies and the two testers (L_1 and L_2) were tested during 1977-78 in Experiment-I and their selfed progenies, $\bar{L}_{1is}$, $\bar{L}_{2is}$ and $\bar{L}_{3is}$ during 1978-79. The selfed progenies, L_1 and L_2 testers and P_i lines were grown in two environments created by two different sowing dates and hereafter designated as Experiments II and III, respectively. The data recorded on different traits of economic importance were analysed through the triple test-cross technique for the estimation of different genetic parameters. The results obtained from these experiments are presented in the following pages :

4.1 Analysis of Variance

The analysis of variance carried out for testing the performance of testers and P_1 lines with respect to different characters in Experiments II and III is presented in Table 1. The P_1 lines were not grown in Experiment I and, therefore, the testers for their phenotypic differences were tested from the analysis of progenies (Table 2) of triple test-cross and were statistically different for plant height and 100-kernel weight.

In Experiment II, the analysis of variance revealed significant differences among the genotypes (testers and P_1 lines) for all the characters. The item due to genotypes was further partitioned into testers, P_1 lines and 'testers vs P_1 lines' at 1, 9 and 1 degrees of freedom respectively. The testers were statistically different for days to maturity, harvest index, spike length, grain yield and protein content. These were phenotypically extreme for days to maturity, harvest index, grain yield and protein content. The P_1 lines were statistically different for all the characters except grain yield and protein content. The contrast 'tester vs P_1 lines' was significant for days to heading, days to maturity, spike length, spikelets per spike, number of grains per spike, grain yield and protein content indicating overall differences between testers and P_1 lines for these characters.

In Experiment III, significant differences among genotypes were observed for all the characters except days to

Table 1 Analysis of variance of testers and P_i lines for different characters in Experiments II and III
(Mean squares)

Sources of variation	df	Expt	Days to heading	Days to maturity	Plant height	Tillers/plant	Harvest index	Spike length	Spikelets/spike	Grains/spike	100-kernel weight	Grain yield	Protein content
Replicates	2	II	** 25.33	1.33	* 77.09	* 2.05	0.002	0.71	0.15	1.39	* 0.29	* 7.54	** 19.88
Genotypes	11	III	13.03	11.08	3.37	0.30	0.023	* 2.35	1.13	10.86	0.03	* 38.73	0.75
		II	** 25.46	** 15.34	** 220.33	* 0.76	** 0.004	** 3.98	** 3.76	** 32.62	** 0.36	* 3.78	** 7.08
		III	12.88	** 12.61	** 173.12	0.29	0.006	* 2.35	** 3.78	** 37.26	* 0.53	* 21.67	3.88
Testers	1	II	1.50	** 13.50	1.50	0.04	** 0.013	* 1.50	1.21	10.93	0.02	** 18.73	** 21.28
P_i s	9	III	32.67	6.00	6.40	0.24	0.001	0.01	0.01	0.48	0.04	0.06	0.14
		II	** 29.86	** 16.80	** 268.95	* 0.92	* 0.003	** 3.41	* 1.86	16.14	** 0.43	1.61	3.95
		III	12.03	** 14.38	** 209.60	0.32	0.007	** 2.62	** 4.03	** 37.11	* 0.56	* 21.29	4.54
Testers vs P_i s	1	II	** 9.80	** 30.05	1.59	0.01	0.002	** 11.55	** 23.40	** 202.67	0.03	* 8.32	** 21.08
		III	0.67	3.20	11.45	0.09	0.005	* 2.29	* 5.24	** 75.40	* 0.74	* 46.72	1.74
Error	22	II	1.42	1.06	12.54	0.32	0.001	0.24	0.61	5.36	0.08	1.33	1.69
		III	9.88	3.42	4.45	0.14	0.004	0.40	0.49	6.14	0.50	7.62	2.73

* Significant at 5 per cent level
** Significant at 1 per cent level

Table 2 Analysis of variance for different characters in Experiment I

(Mean squares)													
Sources of variation	d.f.	Early vigour	Days to heading	Days to maturity	Plant height	Tillers/plant	Harvest index	Spike length	Spikelets/spike	Grains/spike	100-kernel weight	Grain yield	Protein content
Replicates	2	3.91*	76.07**	11.76	57.99*	8.95	0.002	1.95*	2.76*	89.49	0.01	77.15*	11.97**
Progenies	31	1.62**	25.07**	22.92**	152.63**	4.65	0.003	1.23*	2.72**	100.51*	0.38*	36.19*	10.78**
Error	62	0.50	3.86	6.44	18.26	2.56	0.002	0.38	0.66	47.97	0.14	12.54	1.22

* Significant at 5 per cent level
 ** Significant at 1 per cent level

heading, number of tillers, harvest index and protein content. The partitioning of mean squares due to genotypes in three orthogonal contrasts, i.e. testers, P_1 lines and 'testers vs P_1 lines' revealed that testers did not differ from one another for any character. The P_1 lines were statistically different for all the characters except days to heading, number of tillers, harvest index and protein content. The mean square due to 'testers vs P_1 lines' were significant for spike length, spikelets per spike, number of grains per spike, 100-kernel weight and grain yield, indicating overall significant differences between testers and P_1 s for these characters.

The analysis of variance carried out for normal triple test-cross (Experiment, I, Table 2) indicated significant differences among progenies for all the characters except number of tillers and harvest index. The mean squares due to replicates were significant for all the characters other than days to maturity, number of tillers, harvest index, number of grains per spike and 100-kernel weight.

The analysis of variance for different characters in respect of Experiments II and III is presented in Table 3. In Experiment II, the progenies differed significantly for all the characters except number of tillers and harvest index. A similar situation was noticed for parents and crosses except number of grains per spike in crosses, which was not significant. 'Parents vs crosses' item was significant for

Table 3 Analysis of variance for different characters in Experiments II and III
(Mean squares)

Sources of variation	d f	Expt	Days to head- ing	Days to maturity	Plant height	Tillers/ plant	Harvest index	Spike length	Spike-lets/ spike	Grains/ spike	100-kernel weight	Grain yield	Pro-tain con-tent
Replicates	2	II	52.32**	0.25	196.86**	10.98**	0.002	1.39*	0.66	6.85	0.59**	49.40**	31.23**
		III	9.39	44.06**	8.41	1.79**	0.062	8.58**	3.10*	30.19*	0.39*	67.66**	5.29
Progenies	41	II	25.57**	10.19**	161.35**	0.65	0.003	2.01**	1.67**	15.29**	0.24**	2.57*	6.34**
		III	14.20	8.58**	104.88**	0.32*	0.004	1.83**	2.24**	21.50**	0.37**	14.28*	17.05**
Parents	11	II	25.46**	15.34**	220.33**	0.76	0.004	3.98**	3.76**	32.62**	0.36**	3.78**	7.08**
		III	12.88	12.61**	173.12**	0.29	0.006	2.35**	3.78**	37.26**	0.53**	21.67**	3.88*
Crosses	29	II	24.09**	8.18**	125.12**	0.58	0.003	1.27**	0.92*	9.12	0.16**	2.21*	6.22**
		III	15.19	6.50**	73.92**	0.32*	0.003	1.60**	1.73**	16.21*	0.32**	10.84	22.59**
Parents vs crosses	1	II	69.54**	11.62*	563.07**	1.45	0.002	1.88*	0.20	3.54	1.30**	0.18	1.69
		III	0.06	24.58**	252.10**	0.58	0.006	2.45	0.37	1.64	0.13	32.87*	1.35
Error	32	II	1.76	1.73	13.78	0.42	0.002	0.37	0.50	5.54	0.08	1.35	1.93
		III	12.80	2.73	8.02	0.18	0.003	0.62	0.72	7.86	0.11	8.03	1.87

* Significant at 5 per cent level
** Significant at 1 per cent level

days to heading, days to maturity, plant height, spike length and 100-kernel weight indicating the existence of overall differences between parents and crosses for these characters.

In Experiment III, progenies were statistically different for all characters except days to heading. Significant differences among parents were indicated for all characters except days to flower and number of tillers. The crosses also differed significantly amongst them for all characters except days to heading, harvest index and grain yield. The contrast parents vs crosses was significant for days to maturity, plant height and grain yield.

Existence of significant differences among replicates for most of the characters in both the experiments made the error variance more precise.

4.2 Estimates of Genetic Parameters

The tests $\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$, $\bar{L}_{1is} + \bar{L}_{2is} - 2\bar{L}_{3is}$ and $\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$ were performed to test the adequacy of the simple additive-dominance model and the adequacy of the testers. In the first experiment $\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$ test of epistasis was available which unambiguously detects epistasis but does not give any information about the adequacy of testers. In the second and third experiments the same test holds good on the selfed progenies. This test alongwith the comparison $\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$ was performed in Experiments II and III in order to discriminate between the

true epistasis and the presence of common genes in the testers which also result in the failure of the simple model with $\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$ test. The epistasis mean square for 10 d f was further partitioned into an item, testing epistasis (i) type and an item testing (j and l) type epistasis for 1 and 9 degrees of freedom respectively. Similarly the mean squares due to replicates x epistasis at 20 degrees of freedom were partitioned into replicates x epistasis (i) type at 2 degrees of freedom and replicates x epistasis (j and l) type at 18 degrees of freedom.

The estimates of additive and dominance components of variation were based on the comparisons due to sums ($\bar{L}_{1i} + \bar{L}_{2i}$ and $\bar{L}_{1is} + \bar{L}_{2is}$) and differences ($\bar{L}_{1i} - \bar{L}_{2i}$ and $\bar{L}_{1is} - \bar{L}_{2is}$). The direction of dominance was based on the covariance of sums/ differences tested with the aid of a correlation coefficient $r_{\text{sum/diff}}$ at $n-3$ degrees of freedom. The results of the estimates of different genetic parameters alongwith the genotype x macro-environmental interaction parameters are presented characterwise in the following pages :

4.2.1 Early vigour

Epistasis

The data on this character were recorded in normal triple test-cross progenies tested during 1977-78 in Experiment I. The analysis of variance for the detection of epistasis is

presented in Table 4. The mean squares due to epistasis and its components were not significant.

Additive and dominance components

The analysis of variance for sums and differences is also presented in Table 4. The mean squares due to sums and differences were also not significant. Thus there was no evidence of genetic variation for this character.

4.2.2 Days to 50 per cent heading

Epistasis

The mean squares due to epistasis and its components for days to 50 per cent heading with respect to Experiments I, II and III are given in Table 5. In the progenies of Experiment I epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$) was present. Partitioning of this total epistasis revealed that (1) type epistasis was absent, whereas (1 and 1) type was predominant. For the progenies raised in Experiment II, both the tests, i.e. $\bar{L}_{1is} + \bar{L}_{2is} - 2\bar{L}_{3is}$ and $\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$, applied for the detection of epistasis were significant. On examining the components of epistasis in this experiment, (1) type epistasis was found to be highly significant. Since the epistasis was established by both the tests and it was not possible to draw any definite conclusion about the proper choice of the testers for this character. In Experiment III, both the tests

Table 4 Analysis of variance to test for epistasis, sums and differences in Experiment I for early vigour
(Mean squares)

Item	d f	Early vigour
<u>Analysis of epistasis</u>		
Epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$)	10	0.82
a) Epistasis (<u>1</u>) type	1	1.01
b) Epistasis (<u>j</u> and <u>1</u>) type	9	0.80
Replicates x Epistasis	20	0.54
a) Replicates x Epistasis (<u>1</u>) type	2	0.36
b) Replicates x Epistasis (<u>j</u> and <u>1</u>) type	18	0.57
<u>Analysis of sums</u>		
Replicates	2	0.28
Sums ($\bar{L}_{1i} + \bar{L}_{2i}$)	9	1.17
Sums x replicates	18	0.80
<u>Analysis of differences</u>		
Replicates	2	0.08
Differences ($\bar{L}_{1i} - \bar{L}_{2i}$)	9	0.62
Differences x Replicates	18	0.36

Table 5 Analysis of variance to test for epistasis and its components in Experiments I, II and III for days to heading and days to maturity
(Mean squares)

Item	d f	Days to heading			Days to maturity		
		I	II	III	I	II	III
Test I							
Epistasis ($L_{1i}+L_{2i}-L_{3i}$) [@]	10	7.86**	7.83*	12.35	7.00	4.43	5.63*
a) Epistasis (i) type	1	6.81	25.69**	32.94	13.89	0.27	23.47**
b) Epistasis (j and l) type	9	7.98**	5.85	10.06	6.24	4.89	3.64
Replicates x Epistasis	20	1.88	2.68	11.15	6.17	3.11	2.03
a) Replicates x Epistasis (i) type	2	1.71	0.19	13.71	7.61	0.27	5.41
b) Replicates x Epistasis (.j and l) type	18	1.90	2.97	10.87	6.01	3.43	1.65
Test II							
Replicates	2	-	1.43	10.84	-	0.88	18.23**
Epistasis ($L_{1is}+L_{2is}-P_i$)	9	-	8.42*	16.08	-	6.94**	4.03
Replicates x Epistasis	18	-	2.75	10.89	-	1.69	2.78

[@] $L_{1is}+L_{2is}-2L_{3is}$ for Experiments II and III
 * Significant at 5 per cent level
 ** Significant at 1 per cent level
 - Not estimated

detecting epistasis were not significant meaning thereby the absence of epistasis as well as the adequacy of testers.

Additive and dominance components

The analysis of variance of sums and differences for the progenies tested in all the three experiments are summarized in Table 6. Both the sums and differences mean squares were significant in Experiments I and II, but non-significant in Experiment III. The significance of sums and differences for the progenies of Experiments I and II revealed the presence of both additive and dominance components of genetic variation for this trait. The estimates of D and H derived from the variances of sums and differences of Experiments I and II were biased because of the presence of epistasis. The magnitudes of D components were larger than those of the corresponding H components in both the experiments. The estimates of F obtained from the covariance of sums and differences were not significant in these two experiments indicating ambidirectional dominance. The degree of dominance was in the partial dominance range.

Genotype-environment interaction

The analysis of epistatic effects x environments interaction for days to 50 per cent heading is presented in Table 11. The (i) type epistasis though present in Experiment II and absent in Experiment III, was not detected in the pooled analysis.

Table 6 Analysis of variance of sums and differences and the estimates of different parameters in Experiments I, II and III for days to heading and days to maturity
(Mean squares)

Item	d f	Days to heading			Days to maturity		
		I	II	III	I	II	III
<u>Analysis of sums</u>							
Replicates	2	47.02**	20.85**	5.45	6.95	0.62	38.75**
Sums ($\bar{L}_{1i} + \bar{L}_{2i}$) [@]	9	37.54**	39.42**	20.56	24.36*	19.04**	6.08**
Sums x replicates	18	3.92	2.67	11.08	8.86	1.78	1.45
<u>Analysis of differences</u>							
Replicates	2	5.12	3.05	7.35	5.72	0.62	1.32
Differences ($L_{1i} - L_{2i}$) [@]	9	9.54*	7.40**	11.27	13.10**	3.20**	5.85
Differences x replicates	18	3.47	1.16	15.76	3.37	0.75	3.24
<u>Estimates of parameters</u>							
D		22.41 ± 11.83	24.50 ± 12.40	-	10.34 ± 7.91	11.50 ± 5.99 (16.80)	3.08 ± 1.94
H		4.31 ± 3.09	16.64 ± 9.36	-	6.49 ± 4.18	6.55 ± 4.07 (11.80)	-
F		6.04	46.34	-	20.71	6.33 (6.62)	-
r		- 0.08	- 0.34	-	- 0.29	- 0.10	-
(H/D) ^{1/2}		0.44	0.82	-	0.79	0.75	-

@ $\bar{L}_{1is}$ + $\bar{L}_{2is}$ or $\bar{L}_{1is}$ - $\bar{L}_{2is}$ for Experiments II and III

* Significant at 5 per cent level

** Significant at 1 per cent level

- Not estimated

In parenthesis estimates of D_k , H_k and F_k

However, its interaction with the environment was significant suggesting its sensitivity to varying environments. The presence of (i and l) type epistasis was not indicated. The pooled analysis of the comparison $\bar{L}_{1is} - \bar{L}_{2is} - \bar{P}_i$ reflected similar picture. It, therefore, became evident that the expression of epistasis depended upon the environments. A similar situation was observed for sums (Table 12) where mean square due to sums x environment interaction was significant. Interaction between differences and environments was not significant. The additive genes were, therefore, sensitive to the change in environments. However, in the pooled analysis both sums and differences were non-significant.

4.2.3 Days to maturity

Epistasis

The results of the tests for the presence of epistasis for each of the three experiments are summarised in Table 5. The epistasis was absent in Experiments I and II, whereas, it was significantly indicated in Experiment III by the first test with (i) type epistasis being very prominent. The epistasis detected in Experiment II by the second test, indicated the inadequacy of testers because of the common alleles between them.

Additive and dominance components

The mean squares due to sums and differences for each of the three experiments are presented in Table 6. Both the sums and

differences items were significant in all the three experiments except differences in Experiment III. The estimates of D and H parameters indicated higher magnitudes of D over the H components in Experiments I and II and there was no dominance in Experiment III. The estimates of F component in Experiments I and II were not significant indicating ambidirectional dominance. The estimates of D and H in Experiment I are unbiased, whereas these were biased in Experiment II because of the inadequacy of testers and in Experiment III due to the presence of epistasis. The unbiased estimates of D, H and F were computed for Experiment II and are presented in Table 6. The magnitudes of unbiased components were within the range of the estimates of biased components indicating that the bias caused was not great particularly the bias in the magnitude of D was smaller than that in H.

Genotype-environment interaction

The mean squares due to epistasis ($\underline{i}$) type, ($\underline{j}$ and $\underline{l}$) type and $\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$ were not significant in the pooled analysis (Table 11) though ($\underline{i}$) type was present in Experiment III. The interaction between epistasis ($\underline{i}$) x environment was significant. Similar picture was reflected by the pooled analysis of comparison $\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$. Epistasis for this character was thus dependent on the environment in which the material was raised. The pooled analysis of sums and differences over environments indicated

that environmental effects for sums were significant, whereas, for differences these were non-significant (Table 12). The mean squares due to sums in pooled analysis were not significant, whereas for differences these were significant. The interaction of sums with environments was significant but that of differences non-significant which revealed that additive gene effects of this character were more sensitive to the change in environments, whereas non-additive gene effects were not. The magnitude of the interaction component of sums and environments was so high that the differences due to sums could not be detected in the pooled analysis even though these were significant in both the environments.

4.2.4 Plant height

Epistasis

The mean squares due to replication x epistasis (j and l) type were significant (Table 7) for the progenies raised in Experiments I and II when tested against within families error and, therefore, the other items in the analysis of variance for these experiments were tested against it. However, in Experiment III, all items were tested against the within families error.

The tests applied for the detection of epistasis established its presence in all the three experiments (Table 7). The first test of epistasis was significant in all the three experiments. The second test based on the comparison $\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$

Table 7 Analysis of variance to test for epistasis and its components in Experiments I, II and III for plant height and tillers per plant (Mean squares)

Item	d f	Plant height			Tillers per plant		
		I	II	III	I	II	III
<u>Test I</u>							
Epistasis ($L_{1i}+L_{2i}-2L_{3i}$) [@]	10	43.64**	69.74**	27.98**	3.16	0.68	0.19
a) Epistasis (i) type	1	0.01	97.83*	16.08	2.67	0.24	0.001
b) Epistasis (j and l) type	9	48.49**	66.61**	29.30**	3.21	0.72	0.22
Replicates x Epistasis	20	10.34	11.68	9.32	3.41	0.44	0.26
a) Replicates x Epistasis (i) type	2	8.55	6.69	8.14	2.57	0.10	0.82* ..
b) Replicates x Epistasis (j and l) type	18	10.54**	12.24*	9.45	3.50**	0.48**	0.19 63 ..
Within families error	810	3.17	7.56	7.23	1.26	0.16	0.15
<u>Test II</u>							
Replicates	2	-	23.55	2.70	-	1.58*	0.57
Epistasis ($L_{1is}+L_{2is}-P_i$)	9	-	36.26*	16.21*	-	0.74	0.15
Replicates x Epistasis	18	-	10.82*	4.98	-	0.35*	0.18
Within families	810	-	6.31	6.01	-	0.16	0.14

@ $L_{1is}+L_{2is}-2L_{3is}$ for Experiments II and III
 * Significant at 5 per cent level
 ** Significant at 1 per cent level
 - Not estimated

was also significant in both Experiments II and III. When the first epistatic term was further partitioned into epistasis (i) type and epistasis (j and l) type, it was noted that epistasis (j and l) type was significant in all the three experiments, whereas epistasis (i) type was significant in Experiment II only. Thus the presence of epistasis has been indicated by both the tests. No definite conclusion can be drawn about the adequacy of the testers and, therefore, the estimates of genetical parameters, D and H are likely to be biased by epistasis alone or by the combined effect of epistasis and common genes in the testers.

Additive and dominance components

The analysis of variance for sums and differences (Table 8) for each of the three experiments indicated that mean squares due to sums were significant for all the three experiments, whereas mean squares due to differences were significant only for Experiments I and III. The magnitudes of D and H components were biased to an unknown degree because of the presence of epistasis alone or both epistasis and inadequate testers, in all the three experiments. However, the magnitudes of D components were relatively larger than the corresponding magnitudes of H components in all the three experiments. The estimates of F were non-significant for all the three experiments indicating absence

Table 8 Analysis of variance of sums and differences and the estimates of diflerent parameters in Experiments I, II and III for plant height and tillers per plant
(Mean squares)

Item	d f	Plant height			Tillers per plant		
		I	II	III	I	II	III
<u>Analysis of sums</u>							
Replicates	2	17.99	123.73**	4.56	1.23	5.39	1.46**
Sums ($\bar{L}_{1i} + \bar{L}_{2i}$) [@]	9	251.94**	233.34**	139.48**	8.64*	0.49	0.38*
Sums x replicates	18	17.56**	11.47	4.52	2.64**	0.47**	0.15
Within families	540	2.93	7.87	6.33	1.23	0.16	0.14
<u>Analysis of differences</u>							
Replicates	2	6.02	2.58	39.56*	2.94	0.24	0.46**
Differences ($\bar{L}_{1i} - \bar{L}_{2i}$) [@]	9	75.79*	33.43	23.74*	3.12*	0.67	0.21
Differences x replicates	18	24.49**	15.67*	6.64	1.63	0.46**	0.17
Within families	540	2.93	7.87	6.63	1.23	0.16	0.14
<u>Estimates of parameters</u>							
D		156.25 ± 79.27	147.91 ± 73.37	89.97 ± 43.84	3.99 ± 2.78	-	0.15 ± 0.12
H		34.20 ± 24.43	-	45.60 ± 30.42	0.99 ± 1.04	-	-
F		- 66.76	-	151.22	4.04	-	-
r		0.12	-	- 0.33	- 0.19	-	-
(H/D) ^{1/2}		0.47	-	0.71	0.25	-	-

@ $\bar{L}_{1is} + \bar{L}_{2is}$ or $\bar{L}_{1is} - \bar{L}_{2is}$ for Experiments II and III

* Significant at 5 per cent level

** Significant at 1 per cent level

- Not estimated

of directional dominance. The degree of dominance was in the range of partial dominance.

Genotype-environment interaction

The results of the pooled analysis of variance for different epistatic effects are presented in Table 11. The epistasis (i) type and (j and l) type both were significant which revealed that additive and dominance components and their interactions with environments were confounded by epistatic variation. The interactions, epistasis (i) type x environment and epistasis (j and l) type x environment were not significant thereby indicating that these types of epistases were consistent in their expression for this trait. The comparison $\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$ also reflected similar picture. Both the additive and dominance components were significant in the pooled analysis (Table 12). The additive effect x environment interaction (G_{2D}) was significant, whereas, dominance effect x environment interaction (G_{2H}) was not significant, which suggested that additive component was very much influenced by the environments, whereas, the dominance component was not. Ambidirectional dominance in the range of partial dominance was indicated by the non-significant F estimates.

4.2.5 Number of tillers

Epistasis

The mean squares due to epistasis are presented in Table 7. The two tests applied for the detection of epistasis in all these

three experiments did not reveal its presence for this character. The testers, therefore, were adequate and the estimates of genetic parameters would be unbiased.

Additive and dominance components

The mean squares due to sums and differences are presented in Table 8. The mean squares due to sums were significant for Experiments I and III, whereas, those due to differences were significant for Experiment I only. The genetic components of variation as computed from the variances of sums and differences were unbiased estimates of D and H. The magnitude of D component was higher than that of H component in Experiment I. The F component was not significant. The dominance, therefore, was ambidirectional in partial dominance range for the progenies tested in Experiment I, whereas the whole variation in Experiment III was additive.

Genotype-environment interaction

The analysis of epistatic effects x environments interaction for number of tillers per plant is presented in Table 11. The epistasis (j and l) type was the only component which was statistically significant in the pooled analysis. The interactions of epistatic items with environments were non-significant. The additive variance, dominance variance and their interactions with environments were non-significant in the pooled analysis (Table 12).

4.2.6 Harvest index

Epistasis

The mean squares due to comparisons $\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$, $\bar{L}_{1is} + \bar{L}_{2is} - 2\bar{L}_{3is}$ and $\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$ are presented in Table 9. Both the tests of of epistasis were non-significant for all the three experiments which meant that there was no detectable epistasis and the testers also did not share common alleles and are, therefore, appropriate for this character. However, on partitioning of $\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$ term, epistasis (i) type turned out to be significant in Experiment I only. Thus the genetic parameters for Experiments II and III would not be biased.

Additive and dominance components

The analysis of variance due to sums and differences (Table 10) revealed that their mean squares were not significant. This indicated that neither additive nor dominance variation could be detected for this character.

Genotype-environment interaction

A perusal of the items of the analysis of epistatic effects x environments interaction (Table 11) indicated that mean square due to epistasis (j and l) type was significant when tested against the pooled error mean square, whereas, all other items in the anova were non-significant. Both additive and dominance components as well as their interactions with macro-environments

Table 9 Analysis of variance to test for epistasis and its components in Experiments I, II and III for harvest index and spike length
(Mean squares)

Item	d.f.	Harvest index			Spike length		
		I	II	III	I	II	III
Test I							
Epistasis ($L_{1i}+L_{2i}-2L_{3i}$) [@]	10	0.004	0.002	0.002	0.49*	0.48	0.99*
a) Epistasis (i) type	1	0.011*	0.001	0.0001	0.01	0.002	0.0002
b) Epistasis (j and i) type	9	0.003	0.002	0.002	0.54*	0.53	1.10*
Replicates x epistasis	20	0.001	0.001	0.002	0.21*	0.57	0.37*
a) Replicates x Epistasis (i) type	2	0.001	0.001	0.002	0.43**	0.39	0.56*
b) Replicates x Epistasis (j and i) type	18	0.002	0.001	0.002	0.18	0.59**	0.35
Within families	810	-	-	-	0.12	0.17	0.22
Test II							
Replicates	2	-	0.0001	0.009*	-	0.22	0.96
Epistasis ($L_{1is}+L_{2is}-P_i$)	9	-	0.0012	0.002	-	0.39	0.94
Replicates x Epistasis	18	-	0.003	0.003	-	0.42	0.91
Within families	810	-	-	-	-	0.15	0.18

@ $L_{1is}+L_{2is}-2L_{3is}$ for Experiments II and III

* Significant at 5 per cent level

** Significant at 1 per cent level

- Not estimated

Table 10 Analysis of variance of sums and differences and the estimates of different parameters in Experiments I, II and III for harvest index and spike length
(Mean squares)

Item	d f	Harvest index			Spike length		
		I	II	III	I	II	III
Analysis of sums							
Replicates	2	0.001	0.001	0.025	1.35	0.98	4.04**
Sums ($\bar{L}_{1i} + \bar{L}_{2i}$) [@]	9	0.003	0.004	0.003	1.67	2.42**	1.97
Sums x replicates	18	0.003	0.003	0.003	1.33**	0.47**	0.88**
Within families	540	-	-	-	0.12	0.17	0.21
Analysis of differences							
Replicates	2	0.003	0.002	0.004	0.26	0.34	0.18
Differences ($\bar{L}_{1i} - \bar{L}_{2i}$) [@]	9	0.002	0.003	0.006	0.31	0.31	0.82
Differences x Replicates	18	0.002	0.002	0.004	0.31**	0.28	0.86**
Within families	540	-	-	-	0.12	0.17	0.21
Estimates of parameters							
D		-	-	-	-	1.30 ±0.76	-
H		-	-	-	-	-	-
F		-	-	-	-	-	-
r		-	-	-	-	-	-
(H/D) ^{1/2}		-	-	-	-	-	-

@ $\bar{L}_{1is} + \bar{L}_{2is}$ or $\bar{L}_{1is} - \bar{L}_{2is}$ for Experiments II and III

* Significant at 5 per cent level

** Significant at 1 per cent level

- Not estimated

Table 11 Analysis of epistatic effects x environments interaction for different characters
(Mean squares)

Item	d f	Days to heading	Days to maturity	Plant height	Tillers/ plant	Harvest index
<u>Test I</u>						
Epistasis (i_i) type	1	0.23	9.34	96.62**	0.10	0.0001
Epistasis (i_i) x Environments	1	58.40*	14.40*	17.29	0.13	0.0002
Replicates within environments	4	6.91	2.84	7.41	0.46	0.0001
Epistasis (j_i and i_i) type	9	2.92	4.63	84.71**	0.75*	0.0031*
Epistasis (j_i and i_i) x Environments	9	12.99	3.92	11.20	0.19	0.0008
Pooled error	36	6.92	2.54	10.85	0.34	0.0013
	45	8.13	2.82	10.92	0.31	0.0012
<u>Test II</u>						
Environments	1	1242.94**	1536.09**	462.72**	1.04	0.0058
Replicates within environments	4	6.14	9.56	13.12	1.07*	0.0047
Epistasis ($L_{1is} + L_{2is} - P_i$)	9	8.43	5.30	44.37**	0.39	0.0013
Epistasis x Environments	9	16.08*	5.68*	8.10	0.50	0.0018
Pooled error	36	6.82	2.24	7.90	0.27	0.0025
	45			7.94	0.31	0.0023

* Significant at 5 per cent level
** Significant at 1 per cent level

Table 12 Analysis of sums x environments and differences x environments interaction and the estimates of different parameters
(Mean squares)

Item	d f	Days to heading	Days to maturity	Plant height	Tillers/ plant	Harvest index
<u>Sums x Environments</u>						
Environments	1	8517.68**	8003.33**	1092.51**	19.20**	0.0132*
Replicates within environments	4	13.15	19.68	64.15	3.43**	0.0129 *
Sums	9	24.13	15.87	354.93**	0.30	0.0036
Sums x Environments	9	35.84**	9.24**	17.89*	0.56	0.0031
Pooled error	36	6.87	1.62	7.99	0.31	0.0029
	45	-			0.36	0.0029
<u>Differences x Environments</u>						
Environments	1	6.08	0.30	32.14	1.32	0.0015
Replicates within environments	4	5.20	0.97	21.07	0.35	0.0030
Differences	9	6.83	5.48 *	45.63**	0.49	0.0033
Differences x Environments	9	11.83	3.58	11.54	0.38	0.0051
Pooled error	36	8.46	1.99	11.15	0.32	0.0030
	45	9.13	2.31	11.23	0.33	0.0034
<u>Estimates of parameters</u>						
D		-	-	112.34	-	-
H		-	2.53	45.45	-	-
G _{2D}		19.31	5.08	6.59	-	-
G _{2H}		-	-	-	-	-
F		-	-39.76	288.49	-	-
r		-	0.53	-0.28	-	-
(H/D) ^{1/2}		-	-	0.64	-	-

* Significant at 5 per cent level
 ** Significant at 1 per cent level
 - Not estimated

were also non-significant (Table 12) which indicated that there was no detectable genetic variation present for this character.

4.2.7 Spike length

Epistasis

The estimates due to epistasis and its components are given in Table 9. Of the two tests employed for the detection of epistasis, only the first test indicated its presence for the progenies tested in Experiments I and III, whereas there was no detectable epistasis in the progenies grown in Experiment II. The significance of epistasis was adjudged considering replicates x epistasis item as an error because it was found to be significant when tested against within families error. The further partitioning of the epistasis in first test revealed that epistasis (j and l) type was significant for both the experiments, whereas its component partner epistasis (i) type was not significant indicating that combined effect of additive x dominance and dominance x dominance type of non-allelic interactions was important in the manifestation of this character.

Additive and dominance components

The mean squares due to sums and differences for each of the three experiments were not significant except sums in Experiment II (Table 10) which was significant. The only

significant component of genetic variation was D for Experiment II. The component D was an unbiased estimate of genetic variation for this character because of the absence of epistasis.

Genotype-environment interaction

The genotype-environment interaction was absent (Table 19, 20) for all the components. However, only component ($\underline{j}$ and $\underline{l}$) epistasis was indicated among the main effects.

4.2.8 Number of spikelets per spike

Epistasis

The mean squares due to epistasis and its components are presented in Table 13. The epistasis was indicated by the first test in Experiments I and II only, whereas the second test failed to detect its presence in both Experiment II and III. The total epistasis as detected in the first test was partitioned into epistasis ($\underline{i}$) type and epistasis ($\underline{j}$ and $\underline{l}$) type and it was observed that both types of epistases were significant. Epistasis ($\underline{i}$) type was predominant. The estimates of genetic parameters would be biased due to the presence of epistasis in Experiments I and II. However, the main effects D and H would be unbiased in Experiment III.

Additive and dominance components

The mean squares due to sums were significant in all the three experiments, whereas mean squares due to differences were

Table 13 Analysis of variance to test for epistasis and its components in Experiments I,II and III for spikelets per spike and grains per spike
(Mean squares)

Item	d f	Spikelets per spike			Grains per spike		
		I	II	III	I	II	III
Test I							
Epistasis ($L_{1i}+L_{2i}-2L_{3i}$)@	10	1.02**	1.41**	0.78	58.64	11.89*	6.33
a) Epistasis (i) type	1	4.11**	4.14**	2.76	42.63	30.42 *	31.92*
b) Epistasis (i and j) type	9	0.68**	1.10**	0.56	60.41	9.83	3.48
Replicates x Epistasis	20	0.34	0.37	0.76	48.55	4.23	6.79
a) Replicates x Epistasis (i) type	2	0.01	0.24	0.68	201.01	2.35	6.32
b) Replicates x Epistasis (i and j) type	18	0.37	0.39	0.77*	31.61	4.44	6.84
Within families	810	0.34	0.39	0.40	-	-	-
Test II							
Replicates	2	-	0.27	0.80	-	2.46	5.61
Epistasis ($L_{1is}+L_{2is}-P_i$)	9	-	0.51	0.90	-	5.49	10.87
Replicates x Epistasis	18	-	0.70	1.04	-	6.60	10.24
Within families	810	-	0.36	0.38	-	-	-

@ $L_{1is}+L_{2is}-2L_{3is}$ for Experiments II and III
 * Significant at 5 per cent level
 ** Significant at 1 per cent level
 - Not estimated

significant only in Experiment III (Table 14). The estimates of D component were biased in Experiments I and II because of the presence of epistasis, whereas, these estimates from Experiment III were unbiased. In Experiment III the magnitude of D component was lower than the corresponding H component. The component F was not significant. The degree of dominance was in overdominance range for Experiment III. For Experiment I, the dominance variance ($\sigma_{\bar{d}}^2$) was non-significant, whereas the component F significant. This is trivial and arose as a result of sampling error.

Genotype-environment interaction

The analysis of epistatic effects x environments interaction is presented in Table 19. The epistasis ($\bar{i}$) type was significant for this character and all other items of analysis of variance were non-significant which indicated that additive components and their interactions were confounded by epistatic variation. The perusal of the interactions of sums and differences with the environment (Table 20) revealed that sums x environments interaction was significant, whereas all other items were non-significant. The additive effects were highly influenced by the environment such even when detected in both the experiments individually, its expression was not detectable in the pooled analysis.

Table 14 Analysis of variance of sums and differences and the estimates of different parameters in Experiments I, II and III for spikelets per spike and grains per spike
(Mean squares)

Item	d f	Spikelets per spike			Grains per spike		
		I	II	III	I	II	III
<u>Analysis of sums</u>							
Replicates	2	1.06	0.75	2.10	35.19	8.19	22.53*
Sums ($L_{1i}+L_{2i}$) [@]	9	5.87**	1.04**	1.95*	180.86*	11.99	20.17*
Sums x Replicates	18	1.06**	0.54	0.68*	55.44	5.41	5.96
within families	540	0.35	0.39	0.41	-	-	-
<u>Analysis of differences</u>							
Replicates	2	0.74	0.48	0.16	9.07	8.82	1.08
Differences ($L_{1i}-L_{2i}$) [@]	9	0.22	0.34	1.22*	61.96	2.60	11.62
Differences x Replicates	18	0.40	0.27	0.65	35.40	3.48	5.94
Within families	540	0.35	0.39	0.41	-	-	-
<u>Estimates of parameters</u>							
D		3.21 +1.86	0.33 +0.35	0.85 +0.63	83.62 +58.16	-	9.47 +6.47
H		-0.12 +0.11	-	1.53 +1.64	-	-	-
F		-	-	-1.59	-	-	-
r		-0.74*	-	0.13	-	-	-
(H/D) ^{1/2}		-	-	1.34	-	-	-

@ $L_{1is}+L_{2is}$ or $L_{1is}-L_{2is}$ for Experiments II and III

* Significant at 5 per cent level

** Significant at 1 per cent level

- Not estimated

4.2.9 Number of grains per spike

Epistasis

The mean squares due to epistasis and its components for number of grains per spike are presented in Table 13. Two tests were applied for the detection of epistasis in all the three experiments. Epistasis was detected by the first test in Experiment II only. However, on partitioning of this epistasis into its components, (i) type epistasis also turned out to be significant in Experiment II as well as in Experiment III. The components of genetic parameters would be unbiased for Experiment I but biased for Experiment II.

Additive and dominance components

The mean squares due to sums and differences are provided in Table 14. A perusal of the analysis of variance revealed that the mean squares due to sums were significant for Experiments I and III. The mean squares due to differences were non-significant for all the three experiments. The estimates of D components were, therefore, unbiased in Experiment I where epistasis was absent. The estimates of component F were non-significant for all the three experiments.

Genotype-environment interaction

The analysis of epistatic effects x environments interaction is presented in Table 19. The epistasis (i) type was

significant for this character which indicated the confounding of additive effects by epistatic variation. Other items of the analysis of variance were not significant. The additive and dominance components were also not significant (Table 20) in the pooled analysis. The interaction of additive type of gene action with environment was significant which indicated the sensitivity of additive effects to the environmental variations.

4.2.10 100-kernel weight

Epistasis

The mean squares due to epistasis and its components are given in Table 15. Two tests were applied to test the significance of epistasis. The mean squares due to epistasis were significant for Experiment II through first test and for experiment III through the second test. The mean squares due to epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$) were non-significant for Experiments I and III. Further partitioning of total epistasis in the first test indicated that (j and l) type epistasis was significant in Experiments II and III. Epistasis (j and l) type, therefore, was of considerable importance for this trait. The absence of epistasis in Experiment I would allow the estimation of unbiased genetic components. The estimates of genetic components of variation would be biased in Experiment II because of the presence of non-allelic interactions. The significance of

Table 15 Analysis of variance to test for epistasis and its components in Experiments I, II and III for 100-kernel weight and grain yield per plant
(Mean squares)

Item	d f	100-kernel weight			Grain yield per plant		
		I	II	III	I	II	III
Test I							
Epistasis ($L_{1i}+L_{2i}-2L_{3i}$) [@]	10	0.25	0.30*	0.21	47.78**	1.38	11.32
a) Epistasis ($\underline{i}$) type	1	0.06	0.001	0.04	26.07	0.14	8.58
b) Epistasis ($\underline{j}$ and $\underline{l}$) type	9	0.28	0.33*	0.23*	50.19**	1.52	11.62
Replicates x Epistasis	20	0.16	0.10	0.09	10.85	1.29	5.49
a) Replicates x Epistasis ($\underline{i}$) type	2	0.45*	0.01	0.05	17.37	0.89	0.75
b) Replicates x Epistasis ($\underline{j}$ and $\underline{l}$) type	18	0.12	0.11	0.09	10.13	1.33	6.02
Test II							
Replicates	2	-	0.02	0.09	-	6.79*	5.56
Epistasis ($L_{1is}+L_{2is}-P_i$)	9	-	0.14	0.35*	-	1.29	10.69
Replicates x Epistasis	18	-	0.09	0.13	-	1.26	7.89

@ $L_{1is}+L_{2is}-2L_{3is}$ for Experiments II and III

* Significant at 5 per cent level

** Significant at 1 per cent level

- Not estimated

second test in Experiment III established the inadequacy of testers. However, the bias arising due to the sharing of common genes by the testers can be removed and unbiased parameters estimated.

Additive and dominance components

The mean squares due to sums and differences are summarized in Table 16. The mean squares due to sums were significant for all the three experiments, whereas mean squares due to differences were non-significant. The D component was unbiased for Experiments I and III and biased to an unknown degree in Experiment II.

Genotype-environment interaction

The various epistatic x environments interaction items are presented in Table 19. It was noted that none of the items were significant except epistasis x environment interaction in the second test. The mean squares due to sums, differences and their interactions with environments are provided in Table 20. The mean squares due to sums and differences were not significant in the pooled analysis. The sums x environments interaction was significant which revealed the sensitivity of additive gene action to the varying environments.

Table 16 Analysis of variance of sums and differences and the estimates of different parameters in Experiments I, II and III for 100-kernel weight and grain yield
(Mean squares)

Item	d f	100-kernel weight			Grain yield per plant		
		I	II	III	I	II	III
Analysis of sums							
Replicates	2	0.12	0.16	0.20	13.53	24.95**	23.35*
Sums ($\bar{L}_{1i} + \bar{L}_{2i}$) [@]	9	0.60***	0.17*	0.69**	39.62**	3.13	14.38 ^c
Sums x replicates	18	0.11	0.05	0.14	8.17	1.55	5.94
Analysis of differences							
Replicates	2	0.003	0.16	0.28	19.91	0.37	3.45
Differences ($\bar{L}_{1i} - \bar{L}_{2i}$) [@]	9	0.09	0.13	0.15	39.11*	1.89	7.75
Differences x Replicates	18	0.15	0.10	0.14	13.41	1.38	13.17
Estimates of parameters							
D		0.32 +0.18	0.03 +0.07	0.37 +0.22 (0.56)	20.97 +12.58	-	5.63 +4.55
H		-	-		17.13 + 8.94	-	-
F		-	-	-	45.37	-	-
r		-	-	-	-0.29	-	-
(H/D) ^{1/2}		-	-	-	0.90	-	-

@ $\bar{L}_{1is} + \bar{L}_{2is}$ or $\bar{L}_{1is} - \bar{L}_{2is}$ for Experiments II and III

£ Significant at 10 per cent level

* Significant at 5 per cent level

** Significant at 1 per cent level

- Not estimated

In parenthesis estimate of D_k

4.2.11 Grain yield per plant

Epistasis

The results of the analysis of variance for the detection of epistasis are summarized in Table 15 for all the three experiments. The first test was significant in experiment I and non-significant in Experiments II and III. Further partitioning of total epistasis in Experiment I revealed that epistasis (j and l) type was predominant for this trait. Both the tests for detection of epistasis were non-significant in Experiments II and III which revealed that the testers did not share the common alleles for this character besides the absence of epistasis in this material.

Additive and dominance components

The mean squares due to sums and differences are presented in Table 16. These were significant for Experiment I and non-significant for Experiments II and III. However, mean square due to sums in Experiment III was significant at a probability level between 5 to 10 per cent. The genetic parameters estimated for Experiment I were biased to an unknown degree because of the presence of non-allelic interactions. The additive component D was higher in magnitude over the dominance component H. The component F was non-significant which indicated the ambidirectional dominance. The degree of dominance was in the complete dominance range for this character in Experiment I.

Genotype-environment interaction

The epistatic effects x environments interaction parameters for grain yield are presented in Table 19. The examination of the different items in the analysis of variance table revealed that none of the epistatic and interaction items were significant for this trait. The mean squares due to sums, differences and the mean squares due to their interaction parameters in the pooled analysis are presented in Table 20. Mean square due to sums was significant, whereas, none of the other item of biometrical genetical interest was significant. The additive effect was detected in the pooled analysis, whereas it was not detected in the individual environments.

4.2.12 Protein content

Epistasis

The mean squares due to epistasis are given in Table 17. Both the tests applied for detecting epistasis revealed its presence in all the three experiments. Further partitioning of epistatic item in the first test indicated that both (i) and (j and l) types of epistasis were very conspicuous and important in all the three experiments except (i) type epistasis in Experiment II. The significance of second test in Experiments II and III besides establishing the existence of non-allelic interaction suggested the uncertainty of the proper choice of testers.

Table 17 Analysis of variance to test for epistasis and its components in Experiments I, II and III for protein content

(Mean squares)

Item	d f	Protein content		
		I	II	III
<u>Test I</u>				
Epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$) [@]	10	11.72**	9.59**	15.06**
a) Epistasis (<u>i</u>) type	1	4.97*	1.17	19.67**
b) Epistasis (<u>j</u> and <u>l</u>) type	9	12.47**	10.52**	14.55**
Replicates x Epistasis	20	1.16	0.56**	1.10
a) Replicates x Epistasis (<u>i</u>) type	2	1.75	4.33**	1.72
b) Replicates x Epistasis (<u>j</u> and <u>l</u>) type	18	1.10	0.11	1.03
<u>Test II</u>				
Replicates	2	-	0.75	5.04
Epistasis ($\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$)	9	-	4.77**	7.14*
Replicates x Epistasis	18	-	0.73	2.16

[@] $\bar{L}_{1is} + \bar{L}_{2is} - 2\bar{L}_{3is}$ for Experiments II and III

* Significant at 5 per cent level

** Significant at 1 per cent level

- Not estimated

In such a situation the estimates of genetic parameters are definitely biased by epistasis alone or possibly in combination with the inadequate testers.

Additive and dominance components

The analysis of variance of sums and differences (Table 18) for each of the three experiments indicated that mean squares due to sums and differences were significant in all the three experiments except mean squares due to differences in Experiment II. The estimates of D and H components wherever present were biased to an unknown degree because of the presence of non-allelic interaction in all the three experiments. The comparison between the magnitude of D and H components revealed that D and H were relatively of equal magnitude in Experiment I but the component D was much smaller than the H component in Experiment III. The estimates of F were non-significant for Experiments I and III. The significance of F for Experiment II in the absence of dominance itself was due to sampling error. The range of dominance was partial for Experiment I and overdominant for Experiment III.

Genotype-environment interaction

The pooled analysis of variance for the interaction of epistasis and its components with environments is presented in Table 19. The epistasis (i) and (j and l) types in the first test and epistasis in the second test were not significant. The interactions, epistasis (j and l) x environment in the first

Table 18 Analysis of variance of sums and differences and the estimates of different parameters in Experiments I, II and III for protein content

(Mean squares)

Item	d f	Protein content		
		I	II	III
<u>Analysis of sums</u>				
Replicates	2	3.49	18.42	3.75
Sums ($\bar{L}_{1i} + \bar{L}_{2i}$) [@]	9	15.25**	7.26**	9.05**
Sums x Replicates	18	0.96	0.26	0.99
<u>Analysis of differences</u>				
Replicates	2	4.32	5.01	2.08
Differences ($\bar{L}_{1i} - \bar{L}_{2i}$) [@]	9	11.74**	3.18	49.29**
Differences x Replicates	18	1.51	1.60	2.65
<u>Estimates of parameters</u>				
D		9.52 ±4.79	4.67 ±2.28	5.38 ±2.85
H		7.12 ±3.63	4.21 ±4.24	124.39 ±62.00
F		8.97	31.82	33.00
r		-0.17	-0.83*	-0.20
(H/D) ^{$\frac{1}{2}$}		0.86	0.95	4.81

$\textcircled{a}$ $\bar{L}_{1is} + \bar{L}_{2is}$ or $\bar{L}_{1is} - \bar{L}_{2is}$ for Experiments II and III

* Significant at 5 per cent level

** Significant at 1 per cent level

Table 19 Analysis of epistatic effects x environments interaction for different characters
(Mean squares)

Item	d f	Spike length	Spike-lets/spike	Grains/spike	100-kernel weight	Grain yield	Protein content
Test I.							
Epistasis (I_1) type	1	0.002	6.83**	62.33**	0.02	5.45	5.63
Epistasis (I_1) x Environments	1	0.004	0.07	0.01	0.02	3.27	15.21
Replicates within environments	4	0.47	0.46	4.34	0.03	0.82	3.02
Epistasis (I_1 and I_1) type	9	1.34**	0.77	6.37	0.44	8.16	9.12
Epistasis (I_1 and I_1) x Environments	9	0.30	0.89	6.94	0.11	4.98	11.99**
Pooled error	36	0.47	0.58	5.64	0.10	3.67	0.57
	45	0.44	0.64	5.90	0.10	3.93	..
Test II.							
Environments	1	0.56	0.02	1.04	0.97	638.07 **	0.05
Replicates within environments	4	0.59	0.54	4.03	0.05	5.17	2.89
Epistasis ($L_{1is}+L_{2is}-P_i$)	9	1.05	1.08	10.99	0.21	5.16	5.76
Epistasis x Environments	9	0.27	0.33	5.37	0.23*	6.82	6.14**
Pooled error	36	0.66	0.87	8.42	0.11	4.58	1.45
	45	0.59	0.76	7.81		5.03	

* Significant at 5 per cent level
** Significant at 1 per cent level

Table 20 Analysis of sums x environments and differences x environments interaction and the estimates of different parameters
(Mean squares)

Item	d.f.	Spike length	Spike- lets/ spike	Grains/ spike	100... kernel weight	Grain yield	Protein content
<u>Sums x Environments</u>							
Environments	1	3.96*	0.46	47.88	7.34**	2860.66**	0.06
Replicates within environments	4	2.51*	1.43	15.36	0.18	24.15**	11.08
Sums	9	3.81	1.55	17.33	0.56	11.88**	4.39
Sums x Environments	9	0.58	1.34*	14.83*	0.31*	5.63	11.92**
Pooled error	36	0.68	0.61	5.68	0.10	3.74	0.62
	45	0.66				4.12	
<u>Differences x Environments</u>							
Environments	1	1.16	0.69	6.63	0.12	21.08	3.27 **
Replicates within environments	4	0.26	0.32	4.95	0.22	1.91	3.55 **
Differences	9	0.73	0.68	6.06	0.14	5.64	25.27 **
Differences x Environments	9	0.39	0.89	8.15	0.14	3.99	27.19**
Pooled error	36	0.56	0.46	4.71	0.12	7.28	1.92
	45	0.52	0.55	5.40	0.12	6.62	
<u>Estimates of parameters</u>							
D		-	-	-	-	2.08	-
H		-	-	-	-	-	-
G ₂ D		-	0.48	6.10	0.14	-	7.53
G ₂ H		-	-	-	-	-	67.39
F		-	-	-	-	-	-
r		-	-	-	-	-	-
(H/D) ^{1/2}		-	-	-	-	-	-

* Significant at 5 per cent level
 ** Significant at 1 per cent level
 - Not estimated

test and epistasis x environment in the second test were significant which indicated the sensitivity of these types of epistases to the environmental differences. The interaction term was so high that epistasis recorded in the individual environments vanished in the pooled analysis. The mean squares due to sums, differences and their interactions with environments in the pooled analysis are presented in Table 20. The mean squares due to the interaction of sums and differences with environments were significant. This indicated that additive and dominance components of genetic variation are affected by the fluctuations in environments. The interaction was so high that in the pooled analysis the additive variance could not be detected though present in the individual experiments.

DISCUSSION

There has been a considerable improvement in the productivity of wheat during the last 15 years mainly due to the programmes of varietal improvement and crop management. The pace of progress in further upgrading the yield potential in wheat, as also in most other self-pollinated crops, has rather been slow. Future advances lie in the understanding of the genetics of quantitative characters with the use of the existing concepts of quantitative gene action. The present investigation was, therefore, planned to derive information on the relative magnitudes of additive, dominance and epistatic components of variation and their interactions with environments using triple test-cross technique. The results obtained are discussed.

5.1 Analysis of Variance

The existence of genetic differences among testers, parental lines and their progeny families in various experiments and for different characters were evident from the analyses of variances presented in Tables 1, 2 and 3.

5.2 Epistasis

Most of the designs detecting second degree statistics depend upon the assumption of no epistasis. However, there is no sound biological reason to exclude the possibility of epistasis as a part of genetic system of quantitative characters. The triple test-cross design provides an unambiguous test for the detection of epistasis.

In the present study the test based on comparison $(\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i})$ was applied for the detection of epistasis in normal triple test-cross progenies tested under Experiment I. Tests based on comparisons $(\bar{L}_{1is} + \bar{L}_{2is} - 2\bar{L}_{3is})$ and $(\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i)$ were applied for selfs of the normal triple test-cross grown over two environments under Experiments II and III.

The comparison $(\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i})$ detected the existence of epistasis for days to heading, plant height, spike length, spikelets per spike, grain yield and protein content. Thus epistasis played a significant role in the inheritance of these traits. Chapman and McNeal (1971) observed highly significant epistatic effects for plant height, number of tillers and grain yield. Bhullar et al. (1978) reported the presence of epistasis of duplicate type for protein content. Ketata et al. (1976 a) reported the presence of significant epistasis for heading date, plant height, tiller number, kernels per spikelet and grain yield. Ketata et al. (1976 b) also reported the existence of

significant epistasis for plant height and tiller number. Through a triple test-cross analysis in first backcross populations of four wheat crosses, Singh and Singh (1978 b) pointed out the existence of epistasis for plant height and yield per plant. Therefore, the results on the existence of epistasis in the present material were similar to those of Chapman and McNeal (1971) for plant height and grain yield; Bhullar et al. (1978) for protein content, Ketata et al. (1976 a and 1976 b) for heading date, plant height and grain yield; and Singh and Singh (1978 b) for plant height and grain yield per plant. However, the results of Chapman and McNeal (1971) and Ketata et al. (1976a, b) in respect of number of tillers were not similar to those observed in the present investigation.

Further partitioning of the epistatic term revealed that homozygote x homozygote type of epistasis (i , type) existed in the case of spikelets per spike and protein content only. Although, the general test of epistasis for harvest index did not indicate its presence, yet its further partitioning into (i) and (j and l) types revealed significant (i) type of epistasis. Bhatt (1977) and Gill et al. (1978) have observed additive x additive gene effects to be more important for the inheritance of harvest index. A significant contribution of (j and l) type of epistasis was observed for plant height, spike length, spikelets per spike, grain yield and protein

content in the present investigation. The combined effect of additive x dominance and dominance x dominance type of epistasis, therefore, is important in the inheritance of these characters. Singh and Singh (1976) reported the results of modified triple test-cross progenies of two wheat crosses for five characters. They observed that both (i) and (j and l) types of epistases were present for all the five characters, viz. final plant height, ear length, spikelets per spike, grains per spike and grain yield. Singh (1980 b) in a normal triple test-cross, further observed the presence of (i) type epistasis for plant height, 100-kernel weight and yield per plant and of (j and l) type epistasis for plant height and yield per plant. The present studies, therefore, revealed similar (i) type epistatic contribution for spikelets per spike and (j and l) type for plant height, spike length, spikelets per spike and grain yield as reported by Singh and Singh (1976). Similarly, the existence of (i) type and (j and l) type epistases in the present material for plant height and yield per plant was in agreement with that reported by Singh (1980 b). However, the results in the present studies were contrary for 100-kernel weight that did not exhibit (i) type epistasis.

Characters like early vigour, days to maturity, number of tillers, number of grains per spike and 100-kernel weight did not exhibit detectable epistasis. Ketata et al. (1976 a)

in an identical approach, observed absence of epistasis for tiller number, kernels per spike and kernel weight. Absence of epistasis has also been reported by Singh and Singh (1978 b), for 100-kernel weight.

The test based on the comparison $(\bar{L}_{1is} + \bar{L}_{2is} - 2\bar{L}_{3is})$ in Experiment II established the presence of epistasis for days to flower, plant height, spikelets per spike, number of grains per spike, 100-kernel weight and protein content. Epistasis was not present for other traits. A comparison for the expression of epistasis was made between the normal TTC progenies (Expt I) and their selfs (Expt II), grown individually in different experiments to determine the extent of fluctuations for different characters (Table 21). It was observed that total epistasis was present both in normal TTC progenies and their selfed progenies for days to heading, plant height, spikelets per spike and protein content. It was absent under both the situations for days to maturity, number of tillers and harvest index. The characters, spike length and grain yield, exhibited epistasis in the normal TTC progenies, whereas it was not present in the selfs of TTC. Similarly, the normal TTC progenies did not indicate existence of epistasis for number of grains per spike and 100-kernel weight, whereas it was indicated in the selfs for these traits.

Further partitioning of comparison $(\bar{L}_{1is} + \bar{L}_{2is} - 2\bar{L}_{3is})$ in selfed progenies (Expt II) revealed that (i) type

Table 21. Presence and absence of epistasis and its components for different characters in normal TTC (Expt I) progenies and their selfs (Expt II)

Component	Expt	Days to head-ing	Days to maturity	Plant height	Tillers/plant	Harvest index	Spike length	Spike lets/spike	Grains/spike	100-kernel weight	Grain yield	Protein content
$\overline{L}_{1i} + \overline{L}_{2i} - 2\overline{L}_{3i}$	I	+	-	+	-	-	+	+	-	-	+	+
$\overline{L}_{1is} + \overline{L}_{2is} - 2\overline{L}_{3is}$	II	+	-	+	-	-	-	+	+	-	-	+
(<u>i</u>)	I	-	-	-	-	+	-	+	-	-	-	+
	II	+	-	+	-	-	-	+	+	-	-	-
(<u>i</u> and <u>l</u>)	I	+	-	+	-	-	+	+	-	-	+	+
	II	-	-	+	-	-	-	+	-	+	-	+

+ = Epistasis present
- = Epistasis absent

epistasis was existing for days to heading, plant height, spikelets per spike and number of grains per spike, while epistasis (j and l) type was present for plant height, spikelets per spike, 100-kernel weight and protein content. When the epistasis (i) and (j and l) types in the normal TTC progenies were compared with the corresponding estimates in the selfed progenies (Table 21), it was found that the (i) type epistasis was present for spikelets per spike but absent for days to maturity, number of tillers, spike length, 100-kernel weight and grain yield in both Experiments I and II. Epistasis (i) exhibited different behaviour for days to heading, plant height, harvest index, number of grains per spike and protein content in these two types of progeny families. Similarly, the (j and l) type epistasis exhibited its presence for plant height, spikelets per spike and protein content in both normal TTC progenies and their selfs. It was absent for days to maturity, number of tillers, harvest index and number of grains per spike in both experiments I and II. Different type of behaviour was noticed for days to heading, spike length, 100-kernel weight and grain yield; where it was present in the normal TTC progenies (Expt I) and absent in their selfed families (Expt II) except in case of 100-kernel weight, where it was present in the selfed families but absent in the normal TTC progenies.

The above comparisons indicated that the presence and absence of total epistasis did not change in the normal TTC

progenies and their selfs for days to heading, days to maturity, plant height, number of tillers, harvest index, spikelets per spike and protein content. This suggested that the expression of epistasis was not altered in the segregating generations even when the material was grown in different years. However, the change in the expression of epistasis was observed for spike length, number of grains per spike, 100-kernel weight and grain yield in these two types of progeny families. The total epistasis for days to heading in normal TTC progenies was mainly due to additive x dominance and dominance x dominance type, which in the selfed progenies turned to be of additive x additive type, possibly due to the release of transgressive segregates in the selfed progenies. The fluctuations observed for other characters like plant height and protein content are complex in nature and can be mainly attributed to genotype x environment interaction, because these two types of progenies were tested in two different years. The total epistasis for spike length and grain yield in normal TTC progenies was due to ($\underline{1}$ and $\underline{1}$) type of interactions which in the selfed progenies disappeared. Similarly, for 100-kernel weight, total epistasis in normal TTC progenies was not exhibited but this was of ($\underline{1}$ and $\underline{1}$) type in the selfs. This type of epistatic behaviour may be due to genotype x environment interaction, but to substantiate it, further studies are needed. In Experiment III, the comparison ($\bar{L}_{1is} + \bar{L}_{2is} - 2\bar{L}_{3is}$) established epistasis for days

to maturity, plant height, spike length and protein content. Total epistasis was not detected for other characters. Further partitioning of total epistasis in this experiment revealed the presence of (i) type epistasis for days to maturity, number of grains per spike and protein content and of epistasis (j and l) type for plant height, spike length and protein content.

Similar studies on wheat as reported in the present investigations on selfs of TTC are not available. However, Pooni et al. (1980) reported triple test-cross analysis for normal families and their selfs in Nicotiana. They demonstrated that the tests for epistasis based on normal and selfed TTC families involved identical components of epistasis and were equally efficient in detecting additive x additive component of epistasis but differed in smaller coefficients for (j and l) type of epistasis in selfs. They further concluded that in general, selfs provided a less sensitive test for epistasis due to the release of genetic variability following selfing. However, when dealing with pure lines, the loss of sensitivity was much reduced. In the existing study, the normal and selfs of TTC were raised in different years and, therefore, for obtaining reliable picture of the expression of epistasis, further studies are required on such generations where the comparison could be made on both normals and selfs of TTC in one experiment repeated over locations and years. For

plant species in which a single cross-pollination yields one or a few seeds and the self-pollination is easier, the families of TTC can be replaced by their progeny families produced by selfing for growing large populations permitting more replications. If the information on the epistasis detected from normal TTC families and their selfs is similar, it would be worthwhile to avoid the laborious task of producing more F_1 seeds.

The two tests of epistasis, i.e. $\bar{L}_{1is} + \bar{L}_{2is} - 2\bar{L}_{3is}$ and $\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$ jointly detected epistasis for days to heading, plant height and protein content in Experiment II and for plant height and protein content in Experiment III. This suggested the presence of epistasis for these traits but did not rule out the inadequacy of testers. The second test was significant for days to maturity in Experiment II and for 100-kernel weight in Experiment III, suggesting that testers were inadequate for these two traits. Thus the detectable epistasis was not true and was caused by the presence of common genes in the testers in the present material. Such biases in the estimation of epistasis due to inadequacy of testers were observed by Singh (1980 a) for plant height, and peduncle length and by Singh (1980 b) for plant height, length of spike and number of spikelets per spike. Thus the testers used in this study had common genes for days to maturity and 100-kernel weight and hence the estimated genetic parameters were biased.

The bias can be removed by following alternative procedures for estimating the genetical parameters (Jinks and Virk, 1977). The comparison of biased and unbiased components (Table 6 and 16) showed that these did not differ materially from each other. The effect of common genes although detected for these characters was not strong enough to cause an appreciable change in the relative magnitudes of additive and dominance components. Thus the test for detection of inadequacy of testers seems to be very powerful.

Epistasis was detected for almost all the characters studied in the present material except for early vigour and number of tillers. It is, therefore, necessary to take account of this parameter in the inheritance of quantitative characters and the analysis with the assumption of absence of epistasis need to be used with a great caution.

5.3 Additive and dominance components

In the absence of epistasis the additive genetic D and dominance genetic, H components are estimated. These components are estimated with equal precision from the normal triple test-cross families but the coefficient of H is lower in the selfed progenies than that in the normal progenies.

In the presence of epistasis, the expected magnitudes of the estimates of D, H and F components are biased to an

unknown extent. The estimates of D from all sources are equally affected by the (i) type interactions but these estimates from the normal TTC families will be more affected by (j) type interactions than the estimates from their selfs. In contrast, the two sources of estimates of H will be equally affected by (j) type interactions but the estimates from the normal families will be less affected by (i) and more by (l) interactions than those from the corresponding selfed progenies (Pooni et al., 1980).

In the present investigation, the epistatic effects for the normal triple test-cross families (Expt I) were predominant for days to heading, plant height, harvest index, spike length, spikelets per spike, grain yield and protein content. Estimates of both additive and dominance variances were significant for days to heading, plant height, grain yield and protein content. Only additive component was significant for spikelets per spike, whereas for harvest index and spike length neither additive nor dominance variation was present. However, these estimates of additive and dominance components for these traits were biased due to the presence of epistasis.

The epistasis was not detected for early vigour, days to maturity and number of tillers. The additive and dominance components were significant for both of these characters. For early vigour significant genetic variation was not detected. Additive component was reported to be important for days to heading by Bhatt (1972), Paroda et al. (1972) and

Singh et al. (1973). Kandola and Anand (1974) reported the presence of both additive and non-additive types of variances for days to heading and plant height and Aulakh et al. (1973) for grain yield and spikelets per spike. Singh and Singh (1976) observed that the estimates of additive and dominance components for plant height, spike length, spikelets per spike, grains per spike and grain yield were biased because of epistasis.

The relative magnitudes of the estimates of additive, dominance and epistatic components for these characters revealed that days to heading, plant height, spikelets per spike, grain yield and protein content were largely influenced by additive genetic component. The bias in the estimate of D appeared to be due to (j and l) type of interactions for days to heading, plant height, spikelets per spike, grain yield and protein content. Similar observations were reported by Singh and Singh (1976) for plant height, ear length and spikelets per spike. For early vigour, significant genetic variation was not detected, whereas for harvest index and spike length, although the epistasis was detected, yet the additive and dominance components were not significant. These results were contrary to the observations reported by Gupta and Ahmad (1979), for these characters. Both additive and dominance components were significant for days to maturity and number of tillers, whereas component D alone was significant for number of grains per

spike and 100-kernel weight. The estimates of D and H for these characters were unbiased as these were not affected by non-allelic interactions. The present observations were in agreement with those of Quick (1978) and Gupta and Ahmad (1979). Ketata et al. (1976 a) observed additive gene action for spikelets per spike, number of grains per spike and protein content in similar studies on winter wheat. In the studies reported here also, the additive genetic component was significant for these traits. Ketata et al. (1976 a) further gave evidence of dominance gene action for plant height and number of grains per spike. The dominance component of genetic variation was observed for plant height, whereas it was not significant for number of grains per spike in the present studies.

In Experiment II, epistatic variation was recorded for days to heading, plant height, spikelets per spike, number of grains per spike, 100-kernel weight and protein content. The estimates of both D and H components were significant for days to heading and days to maturity. The additive component alone was present for plant height, spike length, spikelets per spike, 100-kernel weight and protein content. For characters like number of tillers, harvest index, number of grains per spike and grain yield, neither additive nor dominance variation was observed.

The comparison of the presence or absence of additive and dominance components of genetic variation for different traits in Experiments I and II was made (Table 22) to determine the extent of variation in these components. It was observed that both additive and dominance components had similar expression in both the experiments for days to heading and days to maturity. The expression of additive component alone was similar in both the progenies for plant height, spikelets per spike, 100-kernel weight and protein content. The dominance component though present in normal TTC progenies for plant height, number of tillers, grain yield and protein content, was not present in selfs for these characters. It was, therefore, observed that the dominance component for the traits studied in the selfed progenies was very small and it was detected only for days to heading and days to maturity.

The literature on the estimates of additive and dominance components of genetic variation on the selfs of TTC progenies in wheat is not available and thus this is the first attempt towards estimation of the genetic components for the normal and the selfed progenies. In general, it was observed that additive component did not diminish in the selfed progenies for the majority of the traits, whereas dominance component diminished in four out of six traits showing its presence.

The additive and dominance components were highly significant in those cases where either epistasis was present

Table 22. Presence and absence of additive and dominance components of genetic variation for different characters in normal TTC (Expt I) progenies and their selfs (Expt II)

Component	Expt	Days to head-ing	Days to maturity	Plant height	Tillers per plant	Harvest index	Spike length	Spike-lets/spike	Grains/spike	100-kernel weight	Grain yield	Protein content
D	I	+	+	+	+	-	-	+	+	+	+	+
	II	+	+	+	+	-	+	+	-	+	+	+
H	I	+	+	+	+	-	-	-	-	-	+	+
	II	+	+	-	-	-	-	-	-	-	-	-

+ Genetic component present
- Genetic component absent

or where the adequacy of testers was not established. Another important feature of this study was that the additive genetic component was consistently larger than the respective dominance genetic, H component for all the characters in all the experiments except spikelets per spike and protein content in Experiment III, where the reverse was true. F component in general revealed ambidirectional dominance for most of the characters.

5.4 Genotype-environment interaction

The selfs from TTC were tested in two environments created by different sowing dates in the same year at one location. The estimates of epistatic effects $\times$ environments, sums $\times$ environments and differences $\times$ environments interactions from the pooled analysis. (Tables 11, 12, 19 and 20) indicated that epistasis (i) type was significant for plant height, spikelets per spike and number of grains per spike and the (j and l) type for plant height, number of tillers, harvest index and spike length. The (i) type epistasis for days to heading and days to maturity interacted with environments. The interaction between epistasis (j and l) type and environments was significant for protein content only. The epistasis (i) type was, therefore, sensitive to environmental differences for days to heading and days to maturity and epistasis (j and l) type was inconsistent for protein content in the

present study. Singh (1980) reported significant interaction of (i) epistasis with environment for plant height and yield per plant and of (j and l) type for plant height and kernel weight in a study on normal TTC progenies. Parallel studies on the selfs of TTC are not available. A different type of situation was exhibited for number of tillers and harvest index where epistasis (j and l) turned out to be significant in the pooled analysis, whereas it was absent in the individual environment. The epistasis $\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$ was observed for plant height only in the pooled analysis. The interaction between $\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$ epistasis and environment existed for days to heading, days to maturity, 100-kernel weight and protein content. Epistasis (i) and (j and l) types for these traits except 100-kernel weight also interacted with environment.

The additive component in the pooled analysis was significant for plant height and grain yield only. The additive component for grain yield in the individual environment although not present, except a borderline significant estimate in one environment, turned out to be significant in the pooled analysis. This was so because the testing of estimate became more powerful due to more precise error obtained in the pooled analysis. The dominance component in the pooled analysis was significant for days to maturity and plant height. The additive genetic component responded significantly to the change in environment for days to heading, days to maturity, plant height,

spikelets per spike, number of grains per spike, 100-kernel weight and protein content. The additive gene action, *additive*, therefore, was very sensitive to environmental differences for majority of the traits. The dominance component was, however, least affected by the differences in environments for all the characters except for protein content. Such studies in the selfed progenies on triple test-cross analysis are not available. However, Singh (1980·b) in a study on normal TTC observed more sensitivity of additive component to macro- as well as micro-environmental differences, whereas dominance component was least sensitive to macro-environmental differences. Paroda and Joshi (1970) reported that variances due to general combining ability interacted **more with the environment** than the specific combining ability for grain yield and other characters. In the present study, interaction of the additive component and environments for days to maturity, number of spikelets per spike, 100-kernel weight and protein content was so large in magnitude that the main additive component detected in the individual environments turned out to be non-significant in the pooled analysis. Similar observations were reported by Matzinger et al. (1971) among burley varieties of Nicotiana tabacum.

5.5 Implications in wheat breeding

For the successful exploitation of genetic variability inherent in the material, the study of genetic parameters (additive, dominance and epistasis) of important quantitative characters was carried out for the formulation of breeding methodology and for the development of material with increased productivity. The superiority of the parents (P_1 lines), used in the present study was adjudged by the deviation of the mean performance of its crosses from the overall mean performance of all the crosses for different characters (Appendix I). Parents Cno-Bb x Cal (7C/Lib.-Inia x Inia Bb), K 4328, Cno x Nar-Chris/Tob-8156-Ceno, Cno-cPo x S_2 ; Ceno-Chris and Inia 'S'-7C were the best combiners for most of the traits.

The superior cross combinations have been identified with the help of deviation of the actual performance from the expected performance for each cross individually in the F_1 and F_2 generations (Appendix II). The extent of depression in F_2 ($\bar{F}_1 - \bar{F}_2$) was obtained by re-scaling the F_1 s' and F_2 s' against the common testers. The significance of depression ($\bar{F}_1 - \bar{F}_2$) was tested with the help of the paired 't' test for all the characters. The paired 't' test revealed that number of grains per spike in F_2 was not different from the F_1 , indicating that the performance of F_2 s' did not show any depression over the F_1 s' for this character. The number of grains per spike is

a very important yield component and this attribute of this character can be of great help for making selection in the segregating generations. The gene action for this trait in normal TTC was predominantly additive, whereas in the selfed progenies additive x additive type of epistasis was also present. The dominance was absent in both the generations. Therefore, selection of crosses showing high grain number and their intermating is likely to be rewarding for exploiting both additive and (i) type interaction components of variation.

Summary of the promising crosses in F_1 , F_2 and the crosses which showed the least depression in F_2 is presented in Table 23. On an overall basis, 11 crosses, viz. Cno x Nar-Chris Tob-8156-Ceno x WG 377, Cno-Bb x Cal(7C/Lib-Inia x Inia Bb) x WG 377, K 4328 x WG 377, Ceno-Chris x WG 377, L 193 x WG 377, Cno x Nar-Chris/Tob-8156-Ceno x HS 13, K 4328 x HS 13, Cno-Bb x Cal (7C/Lib-Inia x Inia Bb) x HS 13, Cno-cPo x S_2 x (WG 377 x HS 13), L 193 x (WG 377 x HS 13) and Cno x Nar-Chris/Tob-8156-Ceno x (WG 377 x HS 13) were promising for many of the important traits. The perusal of the combining ability of lines involved in these promising crosses shows that these involved most of the good combiners.

The most appropriate breeding procedure based upon the results of the present investigation would be the one which accounts for not only the additive and dominance genetic components but also takes into consideration epistatic variation.

Table 23 Some superior crosses for different characters

Characters	F ₁		F ₂	F ₁ - F ₂	
Days to heading	1 x L ₁ ,	6 x L ₁ ,	8 x L ₁ ,	3 x L ₁ ,	2 x L ₂ , 5 x L ₂ ,
	5 x L ₂ ,	3 x L ₃ ,	4 x L ₁ ,	4 x L ₃	
	4 x L ₃		3 x L ₃ ,	2 x L ₃ ,	1 x L ₃
Days to maturity	1 x L ₁ ,	6 x L ₁ ,	2 x L ₁ ,	1 x L ₁ ,	3 x L ₁ , 2 x L ₂
	5 x L ₂ ,	6 x L ₂ ,	3 x L ₃ ,	5 x L ₂ ,	4 x L ₃
	4 x L ₃		3 x L ₃ ,	5 x L ₃	
			2 x L ₁ ,	8 x L ₁ ,	4 x L ₂ ,
Plant height	10 x L ₁ ,	2 x L ₁ ,	8 x L ₁ ,	3 x L ₁ ,	2 x L ₂ , 5 x L ₂ ,
	7 x L ₂ ,	1 x L ₂ ,	4 x L ₂ ,	10 x L ₂ ,	4 x L ₃ , 10 x L ₃
	6 x L ₃ ,	9 x L ₃	9 x L ₃ ,	4 x L ₃	
			2 x L ₁ ,	10 x L ₁ ,	2 x L ₂ , 5 x L ₂ ,
Tillers/plant	7 x L ₁ ,	1 x L ₁ ,	5 x L ₂ ,	5 x L ₁ ,	3 x L ₁ , 3 x L ₂ ,
	8 x L ₂ ,	2 x L ₃ ,	4 x L ₃	7 x L ₂ ,	1 x L ₃ , 9 x L ₃
				9 x L ₃	
Harvest index	8 x L ₁ ,	7 x L ₁ ,	2 x L ₁ ,	3 x L ₁ ,	8 x L ₁ ,
	8 x L ₂ ,	10 x L ₂ ,	3 x L ₃ ,	9 x L ₁ ,	1 x L ₂ , 2 x L ₂ ,
	10 x L ₃			6 x L ₂ ,	1 x L ₃ , 2 x L ₃
Spike length	9 x L ₁ ,	6 x L ₁ ,	8 x L ₂	1 x L ₁ ,	3 x L ₁ , 1 x L ₂ ,
	10 x L ₂ ,	3 x L ₃ ,	10 x L ₃	3 x L ₂ ,	6 x L ₂ , 1 x L ₃ ,
				8 x L ₃ ,	10 x L ₃
Spikelets per spike	9 x L ₁ ,	3 x L ₁ ,	2 x L ₂ ,	3 x L ₁ ,	6 x L ₁ , 3 x L ₂ ,
	1 x L ₃ ,	7 x L ₃		6 x L ₂ ,	6 x L ₃ , 5 x L ₃

....contd....

(ii)...contd....Table 23.

Characters	F ₁		F ₂		F ₁ - F ₂	
Grains/spike	2 x L ₁ , 5 x L ₂ , 3 x L ₃	4 x L ₁ , 9 x L ₂ , 1 x L ₃	3 x L ₁ , 6 x L ₂ , 7 x L ₁ , 2 x L ₂ , 3 x L ₃	3 x L ₁ , 5 x L ₃	1 x L ₁ , 6 x L ₁ , 3 x L ₂ , 5 x L ₂	5 x L ₁ , 2 x L ₂
100-kernel weight	7 x L ₁ , 5 x L ₂	6 x L ₁ , 2 x L ₂ , 3 x L ₃	6 x L ₁ , 3 x L ₂	5 x L ₁ , 4 x L ₃	2 x L ₁ , 2 x L ₂	7 x L ₁ , 6 x L ₂
Grain yield	7 x L ₁ , 5 x L ₂	6 x L ₁ , 6 x L ₂ , 2 x L ₃	9 x L ₁ , 2 x L ₁ , 10 x L ₂ , 2 x L ₃	5 x L ₁ , 3 x L ₂	1 x L ₁ , 5 x L ₁ , 6 x L ₃	3 x L ₁ , 4 x L ₂
Protein content	10 x L ₁ , 4 x L ₂ , 1 x L ₃	7 x L ₁ , 10 x L ₂	10 x L ₁ , 9 x L ₂	4 x L ₁ , 3 x L ₃	4 x L ₁ , 1 x L ₂	9 x L ₁ , 1 x L ₃

.. 112 a:

Simple selection procedures which are conventionally followed in the self-pollinated crops like wheat will not be very rewarding.

The present investigation showed that most of the total genetic variation for almost all the characters studied was associated with significant additive gene action. Of the total 34 cases, additive variation was observed for 24 and, therefore, it should be possible to develop lines or varieties with better yield potential through simple selection procedures. The dominance gene action was also present for days to flower, days to maturity, plant height, number of tillers, grain yield and protein content and recorded in 11 cases out of a total of 34 cases. Under a situation where both additive and dominance components of genetic variation are present, a system of breeding that can take care of both additive and dominance gene effects would be remunerative. The degree of dominance is in the partial dominance range for majority of the characters. Under such a situation, the delayed selection would be fruitful especially when the dominance components would have diminished in the later generations.

The epistasis of both (i) and (j and l) types are governing the expression of several important characters such as days to flower, plant height, spikelets per spike and protein content. The presence of (j and l) types of epistasis along with additive and dominance variation for days

to flower, plant height, grain yield and protein content indicated that all the three kinds of gene actions are playing role in the genetical control of these characters. The difficulty would be encountered in selection and as such standard selection procedures cannot be used for improving such traits in self-pollinated crops. The additive x dominance and dominance x dominance interactions along with dominance component of genetic variation would not be favourable for developing pure lines. However, the dominance and (j and l) types of interactions may be useful in developing hybrids, which are, however, a remote possibility in wheat where production of commercial hybrids is still in the distant future. The conventional breeding approach could take advantage of the additive by additive type of epistasis coupled with additive variation for the improvement of these traits, if selection is delayed until later generations when dominance effects would have diminished. Under such situations, the population improvement methods may be successfully employed for generating additional variability by breaking undesirable linkages through greater recombinations for selection to be more effective.

The epistasis formed an important part of the genetical structure in the present study. Therefore, this component cannot be ignored while formulating breeding plans for the improvement of wheat populations through the manipulation of quantitative traits. If the presence of epistasis is overlooked as is the case with various reports using designs assuming

absence of epistasis, one would not only lose the information about the implications of epistasis but would also obtain biased estimates of additive and dominance components of genetic variation and these biased estimates could lead to faulty breeding procedure.

To derive more reliable estimates of genetic variance components, the testers L_1 and L_2 should be extremes (high versus low selections) for the character under consideration. However, this is not easy to achieve, particularly when several quantitative characters are studied simultaneously. The basic requirement of phenotypically extreme testers is being violated for some of the traits (Jinks and Virk, 1977). Therefore, this type~~x~~ of analysis should be regarded as a means for showing the kinds of gene action involved rather than supplying unbiased estimates for the amounts of additive and dominance variation. In the present study, the normals and the selfs were raised in different years and thus the effects of genotype-environment interaction must have confounded the comparison of estimates derived from these generations. Experiments where these materials are raised in the same environment will be more reliable to determine the utility of the selfed progenies vis-a-vis the normal progenies of the TTC in the case of self-pollinated crops. In practice, one would substitute selfs for the normals only if by so doing more seed would be readily produced and hence larger families and more replications could

be raised for each cross. By doing so, the loss of information about the dominance component H and the loss of sensitivity of the test for epistasis that result from the use of selfs will be partly or wholly restored by the greater replications they make possible. This, however, will not overcome the bias on the estimate of H or the reliability of H to that of D in the presence of epistasis. This can throw additional light on the nature of epistatic contributions and the biases they lead to because epistasis is generally present and should not be ignored.

Chapter VI

SUMMARY

The present investigation was undertaken to investigate the nature of gene action for some agronomic traits and to formulate breeding methodology for wheat improvement. The experimental material consisted of 12 pure-breeding lines of spring wheat. Of these, WG 377 and HS 13 were used as L_1 and L_2 testers and the F_1 between them (WG 377 x HS 13) as L_3 tester. The other 10 P_i lines were crossed to each of the L_1 , L_2 and L_3 testers to produce 30 triple test-cross (TTC) progenies. The 30 TTC progenies and the two testers (L_1 and L_2) were grown during 1977-78 in Experiment I and the selfs of the 30 TTC families, two testers and 10 P_i lines during 1978-79 in two environments created by two different sowing dates in Experiments II and III at the Satyanand Stokes Horticultural Complex, Solan, Himachal Pradesh Krishi Vishva Vidyalaya.

The data were recorded for early vigour, days to flower, days to maturity, plant height, number of tillers per plant, harvest index, spike length, number of spikelets per spike, number of grains per spike, 100-kernel weight, grain yield per plant and protein content. Different components of genetic variation (additive, dominance and epistasis) and

their interaction with the environments based upon the methods given by Kearsey and Jinks (1968), Jinks et al. (1969), Perkins and Jinks (1971), Virk and Jinks (1977) and Jinks and Virk (1977) were studied to investigate the nature of gene action for these traits and to formulate breeding methodology.

The results of analysis of variance indicated significant differences among the genotypes for all the characters in both Experiments II and III, except for days to heading, number of tillers, harvest index and protein content in Experiment III. The testers were statistically different for days to maturity, harvest index, spike length, grain yield per plant and protein content in Experiment II, whereas in Experiment III these were not different for any character. The testers were phenotypically extreme for plant height and 100-kernel weight in Experiment I and for days to maturity, harvest index, grain yield and protein content in Experiment II. The TTC progenies and their selfs tested in Experiments I, II and III differed significantly for all the characters, except for number of tillers and harvest index in Experiment I and for days to heading in Experiment III.

The estimates of epistasis, additive and dominance components of genetic variation were obtained separately for all the three experiments. The interaction of different genetic parameters with environments was studied from Experiments II and III.

Genetic analysis of normal TTC progenies (Expt I) indicated significant epistasis for days to heading, plant height, spike length, spikelets per spike, grain yield and protein content. Further partitioning of total epistasis into (i) and (j and l) types revealed that both of these controlled the expression of spikelets per spike and protein content. Epistasis (i) alone was operative for harvest index while (j and l) type for days to heading, plant height, spike length and grain yield.

In Experiment II, epistasis was present for days to heading, plant height, spikelets per spike , number of grains per spike, 100-kernel weight and protein content. Epistasis (i) and (j and l) both were found to be present for plant height and spikelets per spike. Individually, epistasis (i) was observed for days to heading and number of grains per spike and (j and l) type for 100-kernel weight and protein content.

In Experiment III, significant epistasis was observed for days to maturity, plant height, spike length and protein content. On partitioning total epistasis into its components it was observed that both the types were present for protein content. Epistasis (i) alone was detected for days to maturity and number of grains per spike, whereas (j and l) alone was present for plant height, spike length and 100-kernel weight.

In Experiment I, both additive and dominance components governed the expression of days to heading, days to maturity,

plant height, number of tillers per plant, grain yield and protein content. The additive component alone was observed for spikelets per spike, number of grains per spike and 100-kernel weight, while dominance alone was not operative for any of the traits studied. Ambidirectional dominance in the range of partial dominance was observed for days to heading, days to maturity, plant height, number of tillers and protein content. Grain yield exhibited the absence of directional dominance in complete dominance range.

In Experiment II, both additive and dominance components were present for days to heading and days to maturity. The additive genetic component alone was recorded for plant height, spike length, spikelets per spike, 100-kernel weight and protein content, whereas dominance alone was not present for any of the characters. Absence of directional dominance in the partial dominance range was recorded for days to heading and days to maturity.

In Experiment III, the additive and dominance components were observed for plant height, spikelets per spike and protein content. The additive component alone was operative for days to maturity, number of tillers, number of grains per spike and 100-kernel weight. Ambidirectional dominance was observed for plant height, number of spikelets per spike and protein content. The degree of dominance was in the partial

dominance range for plant height and over-dominance range for number of spikelets per spike and protein content.

The genotype-environment interaction parameters were estimated from Experiments II and III. In the pooled analysis, epistasis (i) type was significant for plant height, spikelets per spike and number of grains per spike, and the (j and l) type for plant height, number of tillers, harvest index and spike length. The epistasis ($\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$) was observed for plant height only in the pooled analysis. The interaction between epistasis (i) and environments was significant for days to heading and days to maturity, whereas interaction between epistasis (j and l) and the environments was present for protein content only. Epistasis ($\bar{L}_{1is} + \bar{L}_{2is} - \bar{P}_i$) was affected by the fluctuation in environment for days to heading, days to maturity, 100-kernel weight and protein content. In the pooled analysis, the additive component was significant for plant height and grain yield while dominance component for days to maturity and plant height. The additive variance was found to be sensitive to environmental fluctuation for days to heading days to maturity, plant height, spikelets per spike, number of grains per spike, 100-kernel weight and protein content. The dominance variance was inconsistent over environments for protein content.

Parental lines Cno-Bb x Cal (7C/Lib.-Inia x Inia Bb)
K 4328, Cno x Nar-Chris/Tob-8156 Ceno, Cno-cPo x S₂, Ceno-Chris

and Inia 'S'-7C were the best combiners for most of the traits. On an overall basis 11 crosses, viz. Cno-x Nar-Chris/Tob-8156-Ceno x WG 377, Cno-Bb x Cal (7C/Lib.-Inia x Inia Bb) x WG 377, K 4328 x WG 377, Ceno-Chris x WG 377, L 193 x WG 377, Cno x Nar-Chris/Tob-8156 - Ceno x HS 13, K 4328 x HS 13, Cno-Bb x Cal (7C/Lib.-Inia x Inia Bb) x HS 13, Cno-cPo x S₂ x (WG 377 x HS 13), L 193 x (WG 377 x HS 13) and Cno-Nar-Chris/Tob-8156-Ceno x (WG 377 x HS 13) were identified for many of the important traits and these involved most of the lines with good combining ability.

The total genetic variation for almost all the characters studied was associated with additive, dominance and epistatic components of genetic variation. The additive variation was recorded in 24 cases, the dominance variation in 11 cases and the epistatic variation in 17 cases out of a total of 34 cases. Under a situation where all the three kinds of gene action are important, standard selection procedures cannot be used for making improvement in self-pollinated crops like wheat. However, the presence of additive and dominance variation could be utilized through delayed selection when the dominance components would have diminished. The epistatic component (i) is manageable through simple selection procedures. The (j and l) types of interactions would not be favourable for developing pure lines, but these may be useful in the population improvement programmes.

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* Original not seen

Appendix I
Deviations of P_i lines for different characters

Sr No	P _i lines	Days to head- ing	Days to matu- rity	Plant height	No. of tillers	Harvest index	Spike length	Spike- lets/ spike	Grains/ spike	100- kernel weight	Grain yield	Protein content
1.	F ₁	0.8	0.2	2.2	-2.2	0.006	0.5	0.5	0.6	-0.22	-3.2	-1.7
	F ₂	-0.3	0.1	3.0	-0.2	0.025	1.4	0.6	1.6	0.06	0.7	-0.2
2.	F ₁	-0.7	-3.4	-1.5	-0.9	0.027	0.6	1.6	8.1	0.01	1.9	-0.1
	F ₂	2.2	-0.5	-2.7	0.1	0.003	-0.1	0.2	0.6	-0.06	0.4	-0.8
3.	F ₁	-4.5	0.6	13.7	0.5	-0.003	-0.6	-1.9	-6.4	0.50	1.5	0.4
	F ₂	-4.1	0.9	11.5	0.2	-0.020	0.2	-0.1	-0.5	0.19	0.7	0.1
4.	F ₁	1.6	-2.6	1.1	0.5	-0.002	0.4	-0.2	3.7	0.14	0.7	-0.3
	F ₂	3.2	-1.1	1.6	0.0	0.011	0.1	0.0	-0.3	0.02	0.0	0.4
5.	F ₁	1.3	0.4	5.8	0.7	0.006	-0.2	-0.6	-7.7	0.50	2.2	0.6
	F ₂	3.2	2.3	5.0	0.4	-0.040	-0.7	-0.5	-2.0	0.01	-1.3	0.8
6.	F ₁	-3.3	-0.1	-0.5	0.2	0.007	-1.2	-1.0	-2.1	-0.36	-2.1	1.9
	F ₂	-4.0	-1.0	-1.8	0.1	0.013	-0.7	0.1	-0.1	-0.10	0.1	1.9
7.	F ₁	1.6	0.4	-5.7	1.0	-0.006	0.0	-0.3	-0.3	-0.30	0.7	-0.3
	F ₂	-0.6	-1.8	-2.7	0.1	0.019	-0.4	-0.3	-0.6	0.04	0.1	-1.3
8.	F ₁	0.0	-0.6	-7.2	-0.5	0.016	0.0	0.2	2.9	-0.02	-1.7	-1.4
	F ₂	-0.1	-0.9	-4.6	-0.1	0.013	-0.2	-0.2	-0.6	-0.02	-0.1	-0.6
9.	F ₁	0.6	1.3	-2.9	0.0	-0.027	0.0	0.6	1.4	-0.22	-0.1	-0.6
	F ₂	-0.7	-0.1	-1.1	0.0	0.006	0.1	0.1	0.0	-0.12	-0.6	1.4
10.	F ₁	2.6	3.6	-5.3	0.9	-0.028	0.8	0.9	-0.3	-0.04	-1.3	0.0
	F ₂	1.3	2.2	-8.1	-0.3	-0.029	0.3	0.4	2.0	0.01	-0.3	-1.0

Appendix II

Deviations of crosses for different characters

Sr No	Cross	Days to heading 3.	Days to maturity 4.	Plant height 5.	lo. of tillers 6.	Harvest index 7.	Spike length 8.	Spike lets/ spike 9.	Grains/ spike 10.	100- kernel weight 11.	Grain yield 12.	Protein content 13.
1.	2.											
1.	1 x L ₁	-2.1	-2.8	5.4	0.5	0.005	0.1	-0.4	-6.1	0.00	-0.1	1.5
	1 x L ₁	0.7	1.9	0.3	0.1	-0.042	0.2	-0.3	-0.6	-0.09	-0.6	0.5
2.	1 x L ₁	1.8	1.8	-3.2	-0.7	0.035	0.2	-0.05	5.8	-0.03	1.7	0.3
	1 x L ₁	-0.8	-1.2	-2.1	0.7	-0.023	0.2	0.0	-0.2	-0.14	0.5	0.3
3.	1 x L ₁	1.2	-0.9	-0.7	-0.3	-0.028	-0.2	0.3	-1.8	-0.08	-0.5	-0.6
	1 x L ₁	3.5	1.1	-5.2	0.2	-0.015	0.5	0.3	1.1	0.00	0.1	0.1
4.	1 x L ₁	-0.2	+0.6	-0.5	-0.8	0.003	0.0	0.0	5.5	0.10	0.7	-2.1
	1 x L ₁	-0.8	-0.3	0.9	-0.1	-0.001	0.1	0.2	0.7	-0.23	0.0	0.0
5.	1 x L ₁	1.1	1.6	-4.9	0.0	-0.010	-0.2	0.0	-2.4	-0.18	-4.2	1.3
	1 x L ₁	0.2	0.3	2.5	0.1	0.012	0.0	-0.4	-0.7	+0.24	0.5	-0.2
6.	1 x L ₁	-2.0	-1.2	5.5	0.2	0.022	0.3	0.0	-0.9	0.17	2.9	0.2
	1 x L ₁	-0.9	-0.4	4.4	-0.2	0.033	-0.3	-0.2	-0.8	0.36	0.6	-1.0
7.	1 x L ₁	-0.5	0.3	6.9	1.6	0.044	0.0	0.1	-1.3	0.34	4.6	1.7
	1 x L ₁	-0.7	-0.2	1.9	-0.7	-0.009	-0.2	0.1	0.9	-0.11	-0.4	0.2
8.	1 x L ₁	-1.3	0.0	-3.0	-0.7	0.070	-0.4	-0.2	4.7	0.01	-1.3	-1.8
	1 x L ₁	-1.8	-0.8	-2.0	-0.6	0.021	0.0	0.0	-0.1	-0.12	-0.6	-0.1
9.	1 x L ₁	0.5	0.7	2.4	0.4	0.005	0.5	0.4	-5.6	0.04	-1.1	-2.1
	1 x L ₁	0.1	0.1	3.1	-0.1	0.033	0.2	0.0	0.1	0.31	0.8	-0.9
10.	1 x L ₁	1.1	0.4	-7.4	-0.8	-0.032	-0.5	0.1	1.7	-0.17	-2.7	2.2
	1 x L ₁	0.4	0.0	-4.5	0.3	-0.013	-0.5	-0.1	-0.4	-0.26	-0.2	0.8

...contd...

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	
11.	1 x L ₂	F ₁	2.5	3.0	-2.6	-1.2	0.005	-0.5	-0.4	-0.8	-0.06	-2.3	-3.5
	1 x L ₂	F ₂	-0.2	-0.5	0.1	0.0	0.038	-0.1	0.0	0.4	-0.08	0.9	-1.1
12.	1 x L ₂	F ₁	-2.0	-2.6	0.7	-0.2	-0.029	-0.2	1.8	-5.8	-0.34	-1.6	-0.1
	1 x L ₂	F ₂	1.6	1.1	-5.7	-0.6	0.010	-0.4	-0.5	-1.0	-0.29	-1.1	0.9
13.	1 x L ₂	F ₁	0.1	2.1	0.2	-0.5	-0.024	-0.3	-0.7	-3.1	0.21	-3.1	0.1
	1 x L ₂	F ₂	-2.1	0.0	3.4	0.1	0.004	0.4	0.6	4.0	0.34	0.9	-1.1
14.	1 x L ₂	F ₁	1.3	0.6	-2.2	-0.1	0.003	-0.1	-0.4	-0.6	-0.08	-2.2	2.6
	1 x L ₂	F ₂	-0.7	-1.3	2.7	-0.3	0.009	-0.3	-0.8	-1.9	-0.05	0.2	2.5
15.	1 x L ₂	F ₁	-2.0	-1.7	4.5	1.6	0.005	0.0	-0.2	3.2	0.19	8.4	-0.5
	1 x L ₂	F ₂	0.3	0.6	-0.1	0.4	-0.020	0.2	-0.3	-1.2	-0.07	-0.5	-0.7
16.	1 x L ₂	F ₁	-1.1	-1.5	-1.3	0.3	0.010	0.3	-0.2	0.2	-0.03	3.0	1.0
	1 x L ₂	F ₂	0.8	0.6	-1.8	-0.3	0.018	0.4	0.1	1.4	-0.13	-0.2	-0.1
17.	1 x L ₂	F ₁	0.5	-0.4	-4.2	-1.3	-0.012	0.2	0.0	2.6	0.09	-1.1	-1.2
	1 x L ₂	F ₂	-0.3	-1.0	0.0	0.4	-0.006	0.2	0.3	0.7	0.09	0.0	0.1
18.	1 x L ₂	F ₁	1.1	1.0	3.2	0.9	0.029	0.4	0.0	-1.6	0.10	1.0	0.2
	1 x L ₂	F ₂	-0.1	0.1	1.5	0.4	-0.025	-0.3	-0.4	-0.9	0.02	-0.3	-1.2
19.	1 x L ₂	F ₁	1.2	0.1	1.0	0.2	0.005	-0.2	-0.1	3.8	0.12	-1.5	0.1
	1 x L ₂	F ₂	-0.2	-1.0	0.0	-0.3	-0.024	0.2	-0.1	0.4	0.02	-0.8	1.0
20.	1 x L ₂	F ₁	-0.8	-0.9	0.9	0.4	0.007	-0.1	0.0	1.7	-0.24	-0.1	1.2
	1 x L ₂	F ₂	0.8	1.0	1.1	0.3	-0.001	0.2	0.5	0.4	0.11	0.8	-0.8
21.	1 x L ₃	F ₁	-1.2	-0.4	-2.6	0.6	-0.008	0.2	0.8	6.8	0.06	2.6	2.0
	1 x L ₃	F ₂	-0.7	-1.6	-1.6	-0.1	0.004	-0.1	0.2	0.3	0.17	-0.3	0.5

....contd....

1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	
22.	1 x L ₃	F ₁	-0.7	0.9	2.5	0.9	-0.005	0.0	-1.3	-0.2	0.37	-0.1	-0.1
	1 x L ₃	F ₂	-0.8	0.0	8.9	-0.1	0.012	0.3	0.5	1.3	0.44	0.8	-1.4
23.	1 x L ₃	F ₁	-2.2	-1.1	0.5	0.6	0.053	0.4	0.5	4.8	-0.15	3.8	0.6
	1 x L ₃	F ₂	-1.5	-1.1	1.7	-0.5	0.012	-0.8	-1.0	-3.0	-0.34	-0.8	0.9
24.	1 x L ₃	F ₁	-2.0	-1.3	2.7	0.9	-0.005	0.1	0.4	-4.9	-0.02	1.5	-0.6
	1 x L ₃	F ₂	1.5	1.6	-3.6	0.2	-0.007	0.4	0.4	1.1	0.27	-0.1	-2.6
25.	1 x L ₃	F ₁	0.0	0.1	0.4	-1.7	0.006	0.1	0.1	-0.8	-0.03	-4.1	-0.7
	1 x L ₃	F ₂	-0.5	-1.1	-2.3	-0.6	0.008	-0.1	0.5	1.8	-0.19	0.2	0.8
26.	1 x L ₃	F ₁	2.3	2.6	-4.0	-0.7	-0.030	-0.6	-0.1	0.7	-0.15	-5.7	-1.2
	1 x L ₃	F ₂	0.0	-0.2	-2.6	0.5	-0.051	-0.1	-0.1	-0.6	-0.25	-0.3	1.0
27.	1 x L ₃	F ₁	-0.6	0.1	-2.7	-0.5	-0.032	-0.2	0.8	-1.3	-0.43	-3.4	-0.5
	1 x L ₃	F ₂	-1.0	1.0	-1.8	0.1	0.014	0.0	-0.5	-1.6	0.02	0.4	-0.5
28.	1 x L ₃	F ₁	-0.4	-0.9	0.0	-0.3	0.011	-0.2	0.3	-3.3	-0.11	0.3	1.7
	1 x L ₃	F ₂	1.8	0.7	0.6	0.1	0.003	0.3	0.4	1.1	0.09	1.0	1.2
29.	1 x L ₃	F ₁	-2.3	-0.8	-3.4	-0.6	-0.010	-0.4	-0.2	1.4	0.02	2.8	1.9
	1 x L ₃	F ₂	0.1	0.9	-3.1	0.3	-0.009	-0.2	0.0	-0.5	-0.33	0.2	-0.2
30.	1 x L ₃	F ₁	-1.0	0.5	6.4	0.3	0.027	0.5	0.0	-3.4	0.41	2.9	3.9
	1 x L ₃	F ₂	2.7	-0.4	3.4	-0.7	0.014	0.3	-0.4	-0.1	0.15	-0.6	-0.1