GENETICS FOR SLOW LEAF-RUSTING AND YIELD RELATED
TRAITS IN BREAD WHEAT (Triticum aestivum L.)

THESIS
SUBMITTED TO THE
JUNAGADH AGRICULTURAL UNIVERSITY
IN PARTIAL FULFILMENT OF THE REQUIREMENTS
FOR THE AWARD OF THE DEGREE
OF
Doctor Of Philosophy (Agriculture) in
Plant Breeding & Genetics

BY

BHATIYA VAJASHIBHAI JIVABHAI
M.Sc. (Agri.)

DEPARTMENT OF AGRICULTURAL BOTANY
COLLEGE OF AGRICULTURE
JUNAGADH AGRICULTURAL UNIVERSITY
JUNAGADH-362 001

MARCH - 2006
Registration No. 04 – 04702 - 2000
**ABSTRACT**

Wheat is the world’s most widely cultivated food crop known for its remarkable adoption to a wide range of environments and its role in world economy. Leaf rust is the major disease causing significant yield loss worldwide. Breeding for slow-rusting has special significance for developing economy were the frequent replacement of cultivars entails enormous expenditure on limited resources. The experimental material comprised of four crosses, namely lok 1 × HD 2189, J 24 × HD 2189, J 24 × HS 347 and kalian sona × HS 347, each with six basic generations (P1, P2, F1, BC1 and BC2) were grown in compact family block design with three replications. Five plants from parents and F1, twenty plants from BC1 and BC2 and fifty plants from F2 generation in each replication were selected randomly for recording the observations on leaf rust, grain yield and filling period related traits. Percent leaf rust infection in term of area under Disease Progress Curve (AUDPC) was recorded on individual plants in all the generations at five different dates. Performance among different generations revealed enough variability in materials studied for slow leaf-rusting. Heterosis over better parent was significant and positive in all the four crosses. Significant and negative inbreeding depression indicated the transgressive segregation toward susceptible reaction in all the crosses.

For slow leaf-rusting, the additive (d) and dominance (h) gene effects were significant for all the four crosses except (h) cross 2 and 4. Among digenic interaction effects, both additive x dominance (j) and dominance x dominance (l) effects were significant for all the crosses, while (i) effect was significant for cross 3 only. The opposite sign of (h) and (l) in cross 1 indicated duplicate epistasis, whereas the same sign of (h) and (l) in cross 3 indicated complimentary epistasis for this trait. High heritability accompanied with high genetic advance was observed in all four crosses. Number of gene groups ranged from zero to 13.

The genetic relationship of per cent leaf rust infection (AUDPC) with days to ear emergence and vegetative period in cross 2 and 4, with plant height in cross 3 and with test weight in cross 2 were significant and positive. While significant and negative correlation of this trait was observed with days to maturity and test weight in cross 4, number of leaves per plant in cross 3, and grain yield per plant in cross 1 and 3. The use of biparental approach or intermating in early segregating generations followed by selection would be highly effective. It should be possible to select high number of gene groups for slow-rusting with better agronomic qualities and potentially durable leaf rust resistance.

The extent of heterosis over mid parent and better parent was poor for different traits, except for grain yield per plant. Significant and positive heterosis, heterosis and inbreeding depression was observed in all the four crosses for grain yield per plant except cross 2 for latter two cases. The inbreeding depression was low to moderate for majority of the characters.

In case of grain yield and filling period related traits, both additive (d) and dominance (h) gene effects were significant for days to ear emergence and vegetative period in cross 1, 2 and 4 for days to maturity in all the crosses, grain filling period in cross 1, 2 and 3 and plant height in cross 1. Only (d) was significant for ear emergence, vegetative period number of leaves per plant and 100-grain weight in cross, 3 besides significance of (d) in cross 2 for 100-grain weight and grain yield per plant as well as in cross 4 for grain filling period. Similarly only (h) was significant for plant height in cross 4, 100-grain weight and grain yield per plant in cross 1 and 4. The additive x additive (i) and dominance x dominance (l) gene interaction influenced almost all the characters in four crosses followed by additive x dominance (j) interaction. Duplicate esistasis was noticed for all the characters in all the crosses except vegetative period in cross 1 indicated that improvement in most of the crosses of the traits delay the crop improvement progress due to presence of duplicate epistasis.

High heritability accompanied with high genetic advance was observed in grain yield indicated additive gene effects. While high heritability accompanied with moderate to low genetic advance was displayed by plant height, days to maturity and vegetative period indicated non-additive gene effects. Number of gene groups varied from zero to 18 for
different character indicated of segregating gene groups that control the trait(s) was varied from characters to characters and from cross to cross for a particular trait due to different genetic material of parental strains involved in various crosses.

Significant and positive correlation was observed between pair of traits like days to ear emergence, days to maturity, vegetative period and grain filling period was observed for most of crosses. Longer grain filling periods was associated with early ear emergence, early maturity, higher grain yield, higher test weight as well as lower vegetative period. Number of leaves per plant had negative correlation with days to ear emergence, days to maturity, grain filling period, plant height and grain yield per plant.

While considering all the parameters, use of intermating among selected plants in early segregating generations followed by selection would be effective which simultaneously exploit both additive and non-additive type of gene action undoubtedly would culminate in significant improvement in grain yield and other important traits in breed wheat.
COLLEGE OF AGRICULTURE
JUNAGADH AGRICULTURAL UNIVERSITY
JUNAGADH

CERTIFICATE –III

Date: 31/07/2006

This is to certify that the thesis entitled “Genetics for slow leaf-rusting and yield related traits in bread wheat (Triticum aestivum L.)” submitted by Mr. VAJASHIBHAI JIVABHAI BHATIYA to Junagadh Agricultural University, Junagadh in partial fulfillment of the requirements for the degree of Ph.D. in the subject of Plant Breeding and Genetics after recommendation by the external examiner was defended by the candidate before the following members of the examination committee. The performance of the candidate in the oral examination was satisfactory, we therefore, recommend that the thesis be approved.

(B. A. MONPARA)
Major Advisor & Training Organizer
Krushi Vigyan Kendra
Junagadh Agricultural University
Keriya Road, Amreli-365 601

(S. C. MANI)

(A. K. JOSHI)
Minor Advisor & Associate Research Scientist Millet Research Station
Junagadh Agricultural University
Jamnagar

(V. P. CHHAVATIYA)
External Member & Professor and Head Department of Agril. Botany College of Agriculture Junagadh Agricultural University Junagadh

(V. P. CHHAVATIYA)
Professor and Head
Department of Agril. Botany College of Agriculture Junagadh Agricultural University Junagadh

Principal & Dean
College of Agriculture, JAU, Junagadh

Approved

(D. B. KUCHADIYA)
Director of Research & Dean P.G.
Junagadh Agricultural University, Junagadh
Dr. B. A. MONPARA  
Major Advisor & Training Organizer  
Krushi Vigyan Kendra  
Junagadh Agricultural University  
Amreli-365 601

CERTIFICATE

This is to certify that the thesis entitled “Genetics for slow leaf-rusting and yield related traits in bread wheat (Triticum aestivum L.)” submitted by Bhatiya Vajashibhai Jivabhai in partial fulfillment of the requirements for the award of the degree of DOCTOR OF PHILOSOPHY (AGRICULTURE) in the subject of Plant Breeding and Genetics of the Junagadh Agricultural University is a record of bonafide research work carried-out by him under my guidance and supervision and the thesis has not previously formed the basis for the award of any degree, diploma or other similar title.

Place: Junagadh
Date: 18/03/2006

(B. A. MONPARA)  
Major Advisor
ACKNOWLEDGEMENT

It gives me pleasure to express my gratitude to Dr. B. A. Monpara, Associate Research Scientist, Agricultural Research Station, Junagadh Agricultural University, Anmreli for his valuable guidance, constant supervision, constructive criticism, encouragement and moral support and help in bringing out the best of my ability in this dissertation.

I am also thankful to the members of my Advisory Committee Dr. V. K. Poshiya, Research Scientist (Chickpea), Pulses Research Station, Junagadh Agricultural University, Junagadh, Dr. A. K. Joshi, Associate Research Scientist, Millet Research Station, Junagadh Agricultural University, Jamnagar, Dr. H. M. Pandya, Retired Research Scientist (Chickpea), Pulses Research Station, Junagadh Agricultural University, Junagadh, Dr. A. M. Parakhia, Professor, Department of Plant Pathology, College of Agriculture, Junagadh Agricultural University, Junagadh, for their keen interest, valuable suggestions and encouragement during the course of this investigation.

I acknowledge with thanks for the facilities provided for build up higher education by Dr. B. K. Kikani, Vice-Chancellor, Junagadh Agricultural University, Junagadh, Dr. D. B. Kuchhadia, Director of Research and Dean P. G. Studies and Dr. Ashok Mishra, Principal, College of Agriculture, Junagadh Agricultural University, Junagadh for their ever willing co-operation, encouragement and care.

I am grateful to Dr. V. P. Chovatia, Professor, Dr. D. R. Mehta, Prof. M. A. Vaddoria, Prof. K. H. Dabhi, Dr. H. L. Dhaduk and all the staff members, Department of Agricultural Botany, College of Agriculture and my friends S/s Dr. M. S. Pithiya, Dr. K. B. Kathiria, K. V. Jivani, D. K. Kadachhi, G. K. Katariya, R. K. Odedara, Dave, Devayatbhai Der, M. H. Vaghela, Shri Jivabhai Chauhan, H. R. Dhameliya, for their co-operation and helpful suggestions in overcoming hurdles during the course of investigation.

I wish to thank heartily Shri H. D. Kavani, Retired Associate Research Scientist, Wheat Research Station, Dr. K. L. Dobariya, Research Scientist (Groundnut), Main Oilseeds Research Station, Junagadh Agricultural University, Junagadh and all the staff members of Wheat Research Station, Junagadh Agricultural University, Junagadh for providing necessary facilities and help during the course of this investigation.

I acknowledge the unstinted help rendered by my beloved daughters Kum. Dhara, son Bhargav, Aum and my beloved wife Nayana for without whoem this piece of work would not have seen light of the day. It is also with profound sincerity that I acknowledge the help, assistance and co-operation of my parents and well wishers whose direct and indirect contributions behind the scene have enabled the successful completion of my investigation.

Place: JUNAGADH

Date: March - 2006

(Bhatiya V. J.)
I. INTRODUCTION

Wheat is the world's most widely cultivated food crop, known for its remarkable adoption to a wide range of environments and its role in world economy is well known. It is the second most important staple food next to rice, consumed by nearly 35 per cent of the world population and providing 20 per cent of the total food calories. In terms of area, wheat occupies about 32 per cent of the total acreage of cereals over the world (Anon., 2000). It is a member of Poaceae family and believed to be originated from the Middle-East region of Asia.

India is the second largest producer of wheat in the world contributing about 72.1 million tones of grains from the area of 26.6 million hectares (Anon., 2005). Uttar Pradesh, Madhya Pradesh, Punjab, Haryana, Rajasthan, Maharashtra and Gujarat are the major wheat growing states of the country. The major growing wheat species in India are bread wheat (Triticum aestivum L.Em.Thell.), macaroni wheat (Triticum durum Desf.) and emmer wheat (Triticum dicoccum schubl.), covering 86, 12 and 2 per cent of total wheat area, respectively. So far ploidy level is concerned, bread wheat comes under the hexaploid wheat with 2n=42 chromosomes and durum and emmer wheat comes under the tetraploid wheat with 2n=28 chromosomes, the basic chromosome number is X=7. Bread wheat is cultivated in all wheat growing area of the country, macaroni wheat mostly grown in the central and southern states.
and also in the north-west, while emmer wheat confined to southern states of the country and in some pockets of Gujarat. Situation of wheat in Gujarat indicates that it contributes 856.6 thousand tones of wheat grains from 435.6 thousand hectares of land under wheat and produces with the productivity of 1967 kg/ha. (Anon., 2003).

Wheat grains are primarily utilized in the form of flour or whole-meal called atta for manufacturing various kinds of food. The flour is the principal ingredient in many kinds of breads, cakes, cookies, crackers, breakfast cereals, etc. It is also used in pancakes, noodles, piecrust, ice-cream cones, pizza, bulgur and other baby foods.

Preparation of various food products mostly depending upon the texture of the grain and protein and gluten content in it. In general, hard textured wheat tend to be high in protein and have strong gluten, which produces a large loaf volume when the flour is backed into bread. The red and white kernel soft textured wheat are used to a lesser extent for making bread and more extensively for making pastry products. The soft wheat tends to be lower in protein and weaker in gluten. The durum wheat has a special importance, which include both red and amber kernel types that are hard to vitreous in texture and are mainly used in the production of semolina products.

One of the most important factors that limits the grain yield in wheat is the damage due to diseases in general and rusts in particular. There are three important rusts occurring in wheat. Black rust (stem rust)
caused by *Puccinia graminis* pers.f.sp. *tritici* Eriks. & E. Henn., yellow rust caused by *Puccinia striiformis* west.f.sp.*tritici* and brown rust (leaf rust) caused by *Puccinia triticina* Eriks. Among these, leaf rust is the major disease causing significant yield loss world wide (Saini *et al.*, 2000). Leaf rust reduces the quantity and composition of assimilates available for grain development and ultimately kernel size, grain yield and protein concentration, thereby income of farmers and the profits of flour mills (Cox *et al.*, 1997).

Attempts have been made for controlling wheat rusts, but the ravages of the rust are still beyond the control. In India, many wheat varieties have been evolved which are genetically resistant to rust diseases, but are very few to meet the requirement of different geoclimatic conditions. In many cases, cultivars became susceptible to new races shortly after their release because the pathogen underwent a rapid evolution of more virulent races in response to high selection pressure on it. Increased awareness of the short lived nature of immune type resistance to wheat rust had led greater interest in some other forms of resistance.

The term slow- rusting was given by Caldwell (1968) as a type of resistance where disease progresses at a retarded rate, resulting in intermediate to low disease levels against all pathotypes of a pathogen. Partial resistance, a synonymous to slow-rusting was explained by Parlevliet (1975) that it is a form of incomplete resistance characterized
by a reduced rate of epidemic development despite a high or susceptible infection type. A similar term, durable resistance was described by Johnson (1981) as type of resistance which remains effective in a cultivar during its widespread cultivation for a long sequence of generations or period of time in an environment favourable to a disease.

Breeding for durable resistance has special significance for developing economy where the frequent replacement of cultivars entails enormous expenditure on limited resources (Sawhney, 1998). Due to technical difficulties in hybrid seed production, the commercial exploitation of heterosis in wheat has limited application. Therefore, the ultimate aim of wheat breeder is to evolve resistance varieties with enhanced yield.

Grain yield is the ultimate product of action and interaction among the component traits. Thus, improvement in component traits would definitely enhance the yield level of the crop. Hybridization between genetically distinct genotypes and selection in segregating is for most to develop cultivars with desirable gene combinations. A genetic improvement in any crop plants depends upon the existence of genetic variability in the base populations on which the selection is to be practiced. Since $F_2$ population form the base materials for selection, it is pertinent to study the extent of variability and nature and magnitude of gene effect in such population to predict the efficiency of early generation selection. Also, segregating populations provide a better material for
correlation studies due to less influence of independent segregation. The understanding of relationship of component traits with yield ensures the effective selection for simultaneous improvement in component characters and thereby yields.

Development of hybrids is an improvement genetic tool in improving yield. However, commercial exploitation of heterosis in wheat has limited application because of technical difficulties encountered in hybrid seed production. It would be helpful to identify superior segregants in early generation. Further, the knowledge on nature and magnitude of gene actions involved in the inheritance of yield and its component characters helps the breeder in deciding breeding strategies to adopt for yield improvement. Therefore, to have the information on genetic nature for slow leaf-rusting and related traits of grain yield and filling period in wheat, the present investigation was undertaken with following objectives.

1. To know the nature of gene actions for slow rusting, grain yield and related traits in bread wheat
2. To determine number of genes and heritability for slow rusting, grain yield and related traits in bread wheat
3. To study the relationship, if any exist, between slow rusting and grain yield related traits in bread wheat
4. To estimate heterosis and inbreeding depression for slow rusting, grain yield and related traits in bread wheat
II. REVIEW AND LITERATURE

The literature pertaining present study on genetics for slow leaf-rusting and yield and its related traits in wheat have been review under the following headings.

2.1 Genetics for slow leaf-rusting and related traits

The development of disease resistance breeding is closely linked with the development of genetics, plant pathology and the progress of plant breeding methods. First cross of wheat based on Mendel’s genetic principles, aiming to transfer disease resistance, was carried out by Biffen (1905). He found monogenic inheritance of yellow rust resistance in wheat. Such inheritance has been latter confirmed in other crops and pathogens. The discovery of physiological races in cereal rusts (Stakman 1914) enabled exact genetic analysis of resistance. Besides studies of inheritance of resistance, the genetics of virulence was often found monogenic (Flor, 1942). From his results on genetics of resistance in flax and virulence in flax rust, Flor (1956) developed the gene for gene hypothesis. Person (1959) demonstrated practical applications of this hypothesis. Polygenic resistance become more popular when Van der Plank (1963) published his analysis and conclusion on vertical and horizontal resistance. He was the first epidemiologist to clearly define
the theoretical basis of concepts of resistance. In the late 1960s and 1970s, there was a revival of the concept of general (race-nonspecific) resistance and its application in crop improvement (Caldwell, 1968). This approach was widely used for breeding leaf rust resistance by Caldwell (1968), stem rust resistance by Borlaug (1954) and yellow rust resistance by Johnson (1981) in wheat. The wide scale application of such a concept in leaf rust resistance commonly known as durable resistance (slow-rusting).

Durable resistance, as defined by Johnson (1981), is that which has remained effective in a cultivar during its widespread cultivation for a long sequence of generations or period of time in an environment favorable to a disease. Durability of disease resistance attracted attention particularly in the last decade when several conferences were devoted to this aspect of resistance (Bartos et al., 2001).

Durable or partially resistant or slow rusting wheat cultivars are suboptimal environments for leaf rust development because they retarded the establishment and reproduction of the fungus. Partially resistant cultivars slow down, but do not completely inhibit, the spread of leaf rust. Partial resistance may be more durable than complete resistance because it places less selection pressure on the pathogen and often genetically more complex than hypersensitivity (Lehman and Shaner 1997).
From the economic view points, rust are most harmful among the diseases affecting wheat crop. Particularly leaf rust (brown rust) *Puccinia triticina* is widely distributed in all the wheat growing zones of northern, eastern and central India (Joshi, 1976). Various estimates of losses due to brown rust epidemics have been made from time to time. Kolmer (1996), reported that wheat cultivars become susceptible to leaf rust regularly and yield loss estimated from 5 to 15 per cent or greater, depending on the stage of crop development when the initial rust infection occur.

The relevant literature on genetics for brown rust (leaf rust) resistance with special reference to slow-rusting in wheat is very scanty. Therefore, similar studies on other cereal rusts have also been reviewed in following paragraphs.

Ohm and Shaner (1976) studied three components of leaf rust like latent period, pustule size and pustules per square centimeter of leaf area for two slow-rusting (Suwon 85 and P 6028) and two fast rusting (Monon and Suwon 92) wheat cultivars in green house and field conditions. In green house experiment, longer latent period, smaller pustule size and less number of pustules per square centimeter of leaf area were in slow-rusting as compared to fast-rusting cultivars. Whereas, in field condition, less leaf rust severity and smaller pustule size was observed in slow-rusting cultivars than fast-rusting cultivars.
Skovmand et al. (1978) studied the inheritance of slow-rusting to stem rust using F_5 progenies of the crosses involving seven spring wheat cultivars mated in all possible combinations without reciprocals. Slow-rusting varied significantly among the parents and among the F_5 progeny of each cross. Positive and negative transgressive segregation occurred in each cross. The genetic control of slow-rusting was predominantly additive and narrow sense heritability was approximately 80 per cent. The number of segregating genes having an effect on slow-rusting was estimated to be 2 to 12 gene pairs depending on the cross. Correlation between slow-rusting and maturity was usually negative but in most crosses the relationship was loose.

Inheritance of rust reactions and their association with other traits was studied by Wells and Cowley (1980). Two dominant gene pairs and one recessive gene pair controlled immunity for leaf rust and stem rust, respectively in variety Hand. Leaf rust resistance was usually found to be associated with large seed and high protein. But no association of these characters was found with stem rust, except in F_3 of one cross.

Ayers et al. (1981) studied inheritance of resistance to stem rust in two crosses involving one slow-rusting spring wheat line FKN and two fast-rusting lines, i.e. W 3498 and 3-106. The progenies in the F_6 generation of these crosses with FKN were studied. The area under the disease progress curve (AUDPC) was used to measure the rate of rusting.
Broad sense heritability estimates were 66 and 52 per cent for FKN x W 3498 and FKN x 3-106 crosses, respectively. AUDPC was significantly associated with some Sr genes and the combinations of these Sr genes.

Kapoor and Joshi (1981) tested six wheat varieties against *Puassginia graminis triticiana*. The variety Sonalika showed slow-rusting reaction as compared to Agra Local, Kharachia, K 68, C 106 and Kalyan Sona. In the similar manner, Gupta and Singh (1982) reported UP 310, Janak, WH 147, GLR-1 and GLR-22 as slow-rusting types as compared to Lal Bahadur and other varieties tested under glass house conditions.

Lee and Shaner (1985a) studied the inheritance of latent period of brown rust in wheat crosses between slow and fast-rusting cultivars inoculating artificially with *Pucinia triticiana* in the green house. Analysis of F₃ families, F₁ and backcrosses of the cross Morocco x SW 72469-6 and L 574-1 x Suwon 92 showed that the long latent period in slow-rusting wheat cultivars, SW 72469-6 and L 574-1 was conditioned by two partially recessive genes with equal effects. Latent period and uredinia size were negatively correlated to each other. The length of latent period in slow-rusting wheat cultivars was governed by 1 to 3 recessive gene pairs with equal effects.

In another study by Lee and Shaner (1985b), they found transgressive segregation for length of latent period in the crosses between six slow rusting wheat cultivars. Most of the genes conditionally
long latent period in these six cultivars differed from each other and showed additive effects. They opined that wheat with very long latent period could be obtained by making cross among different slow-rusting wheat cultivars.

Singh et al. (1986) studied inheritance of component characters of leaf rust through 11x11 half diallel in wheat. Additive effects were found to play major role in the inheritance of latent period and pustule size. The degree of dominance was partial. The heritability in narrow sense was found to be high for both the characters.

Bjarko and Line (1986a) studied six generation, viz., P₁, P₂, F₁, F₂, BC₁ and BC₂ of six crosses made in all possible one way combinations involving three leaf rust resistant (Borach, Wompum, Ward) and one susceptible (Twin) wheat genetic stocks. The inheritance of resistance based on severity of leaf rust measured in term of area under the disease progress curve (AUDPC) was recessive in Borach and partially recessive in Wompum and Ward. The additive gene action exhibited in the crosses between these cultivars indicated that it should be possible to identify progenies with greater leaf rust resistance than that found in the parental cultivars. They further suggested that selection for slow-rusting lines with good agronomic characteristics and potentially durable leaf rust resistance could be possible.
Similarly, another study on inheritance of leaf rust resistance was carried out by Bjarko and Line (1986b) using parental, F1, F2, BC1 and BC2 populations of all possible single crosses involving two slow-rusting, one highly resistance and one susceptible wheat cultivars. Leaf rust severity was measured as area under the disease progress curve (AUDPC) and reported that there were no discrete phenotypic classes in the segregating populations of any cross for this character. Based on quantitative analysis they observed that each plant possessed two or three genes or possibly more genes for slow-rusting. Transgressive segregation for susceptible, but not for resistance, was observed. Narrow sense heritability estimates indicated that selection for lines with increased number of genes for leaf rust resistance could be possible.

Wilson and Shaner (1989) studied seedlings reactions of PI 429155 (slow-rusting and hypersensitive resistance), PI 429007 (susceptible) and their stable selected progenies 83907RC4 (Hypersensitive resistance) and 83907C1 (Slow-rusting) by transplanting into the field at two leaf stage of triticale. Two artificial epiphytotic conditions were provided for disease development. The results indicated 1-2 incompletely dominant genes with major effects for longer latent period in addition to minor genes against leaf rust.

Jacobs and Brores (1989), made crosses between the highly susceptible (Little Club) and the partially resistance (Westphal 12A,
Akabozu and BH 1146) cultivars to obtain F₁, F₂ and backcross generations. Latency period (LP) was determined in plants inoculated at the young flag leaf stage with a monospore culture of race Flamingo of wheat leaf rust. Broad sense heritability of latency period in the F₂ averaged 80 per cent. The genes showed partial to almost complete recessive inheritance. Scaling tests indicated that additive gene action was the most important factor in the inheritance of partial resistance. There were no indications for additive x additive (i), additive x dominance (j) or dominance x dominance (l) interactions. The number of effective genes was estimated as one or two for Akabozu, three or more for Westphal 12A and two or three for BH 1146. The BH 1146 also possessed a (semi) dominant gene for lower infection type, which was temperature sensitive in its expression. The genes of the various parents had unequal effects on latency period.

Eight leaf rust resistant durum cultivars of diverse origin were crossed and backcrossed to a susceptible line, RL 6089 by Zhang and Knott (1990). The seedlings of the F₁, F₂ and BCF₂ generations were tested with race 15 in the greenhouse. Lines carrying single gene for resistance were developed from the backcrosses and tested with race 15 to determine, if any of the parents carry genes for resistance in common. All of the parents carried different genes for resistance. In total, nine
genes were identified in the seven parents. Three of them were dominant and six were recessive.

Kaul et al. (1991) made crosses among 13 leaf rust resistant lines and three testers in line-tester fashion. Variance due to lines were significant for leaf rust resistance, plant height, 100 grain weight and grain yield per plant, whereas variance due to tester was significant for leaf rust resistance, plant height and grain yield per plant. This indicated that the lines and testers differed among themselves in their genetic make up. The estimates of variances due to specific combining ability was more than that of the general combining ability, indicating the predominance of non-additive genetic variance for all the characters studied. They suggested that in addition to resistance, varieties offering good chances of improving other characters of economic importance should be given importance.

The F\textsubscript{6} lines derived from two separate diallel sets and their parents were tested by Das et al. (1992) under artificial epidemics conditions. First diallel set was formed involving one fast-rusting and five slow-rusting wheat genotypes, while another set included one fast-rusting and two slow-rusting cultivars. The area under the disease progress curve (AUDPC) was used to measure rust severity over time. The results showed significant differences in AUDPC among crosses and among progenies within the cross. Predominance of additive genetic variance for
slow-rusting was detected but additive x additive (i) genetic variance also was present. Association between plant height and slow-rusting was observed.

Genetics for leaf rust resistance in wheat was studied by Pawar et al. (1992). Five generations (P₁, P₂, F₁, F₂ and F₃) of two crosses with the combinations of resistance (P-IBW 191) x susceptible (Sonalika) and resistance (P-IBW 191) x moderately susceptible (WH 416) of wheat cultivars were evaluated for disease. The generation means analysis showed that leaf rust resistance was governed by both additive as well as complementary type of gene action and therefore, pedigree method of selection could be useful for developing leaf rust resistant lines.

Field resistance to leaf rust in wheat was studied by Yadav et al. (1992) growing six generations vîz., P₁, P₂, F₁, F₂, BC₁ and BC₂ in 1985-86 and seven generation, vîz., P₁, P₂, F₁, F₂, F₃, BS₁ (B₁ self) and BS₂ (B₂ self) in 1986-87 of a cross HD 2009 x WH 147. Field resistant was found to be partially dominant and controlled by three or more genes. Both additive and non-additive gene effects were important in the inheritance of leaf rust resistant. Additive component maintained similar magnitude in both the years, whereas, magnitudes of non-additive components were variable in different years. The two wheat cultivars namely HD 2009 and WH 147 appeared to have different major / minor genes for field resistant. Leaf rust resistance genes, Lr₁₃, present in both
the parents was found to be ineffective against the Indian leaf rust races. Transgressive segregation for resistance and susceptible reaction was observed in F2 generation.

Dalal and Singh (1994) studied genetics for slow-rusting of bread wheat leaf rust through generation means analysis. Seven generations (two parents, F1, F2, F3, BC1 and BC2) of three crosses (Kalyan Sona x Pavan, Kaylan Sona x WH 147 and K 68 x Veery's) were raised. The results indicated that partial dominance was observed in all the three crosses and the genes causing less disease were dominant over their alleles causing more disease. Duplicate epistasis was found to be present in all the three crosses.

Shaner et al. (1997) studied the progenies of a cross between cultivars CI 13227 (slow-rusting, tall with awns, hair less glumes and late maturing) and Suwon 92 (Fast-rusting, short, awnless, hairy glumes and early maturing). The F6 and F7 families were developed from F2 plants through single seed descent methods by screening for slow-rusting at adult stage. The material consisted of 98 F6 derived F7 recombinant inbred families, parents and a susceptible cultivars was screened for leaf rust in green house by providing artificial epiphytotic conditions. They concluded that four gene pairs with epistasis effect controlled latent period in F7 inbreds. Narrow sense heritability of an F2 individual was fairly high ranging from 64 to 98 per cent. They suggested that selection
for latent period could begin in the F₂ generation, but desirable phenotypes will continue to segregate in later generations from somewhat susceptible plants, so it may be advisable to carry bulk populations for several generations from which fairly homozygous slow-rusting plants may be selected.

Singh et al. (1998) made cross of Pavon 76 (released and slow-rusting wheat) with Jupateco 73s and Avocet s (leaf rust susceptible wheat cultivars). The experiment was tested at two field sites. Evaluation of F₁ plants and parents indicated that the slow-rusting was partially dominant. The F₃ and F₅ lines of these crosses were evaluated for adult plant leaf rust resistant. Segregation in the F₃ and F₅ generations indicated that the resistance was based on two genes with additive effects.

The nature and inheritance of leaf rust resistance of wheat cultivars viz., Monitou, Pavon 76 and Romany against Indian races, namely 12, 77, 77-1, 77-3, 108 and 162 was studied by Saini et al. (1999). The field resistance of cultivars Monitou and Pavon 76 against race 77-1, without evidence of hypersensitive response was conditioned by duplicate genes and it was proposed to be durable. The resistance of Romany in field tests against race 77-1 was also due to duplicate genes but at least one of these genes was hypersensitive in nature.

To determine the nature and number of resistance genes in line the federation *4/kavkaz, this line was crossed with leaf rust susceptible
genotypes Agra Local and WL 711 by Kaur and Saini (2001). The parents, F₁, F₂ and F₃ generations from these crosses were raised and tested at seedling stage in glass house and in opened field in an artificial epiphytotic of race 77-5. One dominant gene was found to be working as seedling resistance genes. While two dominant genes were working for leaf rust resistance at adult stage. Of these two, one was the dominant seedling resistance gene, which remained effective at adult plant stage also and second gene is an adult plant resistance gene that became operative at adult plant stage only. They opined that the line federation *4/kavkaz may find useful in wheat breeding programmes.

Zhang et al. (2001), studied transgressive segregation, heritability and number of gene controlling durable resistance to stripe rust in the cross between one Chinese and two Italian wheat cultivars. Wheat cultivars Libellula (LB), San Pastare (SP) and Xian Nong 4 (XN 4) were durable resistant and Ming Xian 169 (MX 169) was highly susceptible. They evaluated parental, F₁, F₂, F₃ and backcross generations in the field. Transgressive segregation for resistance was observed in the resistance cross resistance crosses of LB x XN 4 and XN 4 x SP, but not in cross LB x SP. This results indicate that (1) the resistance genes in XN 4 are different from those in LB and SP and (2) LB and SP share common resistance genes. LB and XN 4 appears to have 2-3 genes, while SP appears to have 2-4 genes. Transgressive segregation indicated the
expectation of higher level of resistance. Broad sense heritability was high in all the crosses except LB x SP. Narrow sense heritability was higher in LB x MX 169 and SP x MX 169 crosses. The LB x XN 4 and XN 4 x SP crosses showed moderate narrow sense heritability. They suggested that selection in early generations could be effective for the stripe rust resistance in some crosses.

The inheritance of leaf rust resistance of a CIMMYT derived line CIM 25 against the most Indian virulent race 77-5 was studied by Bansal et al. (2004). The line CIM 25 was crossed with a leaf rust susceptible cultivar WL 711 and the F₁, F₂ and F₃ generations from the cross were evaluated at seedling stage in glass house and at adult stage in field conditions for leaf rust infection scores. The low terminal disease severity of CIM 25 line in field tests was ascribed to two dominant genes, one of these genes has been identified to be a hypersensitive seedling resistance gene which remain effective at adult plant stage also. The second gene is the adult plant resistant gene. They opined that this cultivars has Lr34, the only gene so far reported to confer durable resistance to leaf rust. Therefore, the resistance of CIM 25 may be of significance for utilization in wheat breeding programme.

Basandrai et al. (2004) assessed parental F₁ and F₂ generations obtained by crossing of three exotic adult plant resistant cultivars i.e. Chris, Banks and Egret crossed with susceptible cultivars Agra Local for
disease severity under artificial epiphytotic of the race 77A. In addition, the plants in F$_2$ and F$_3$ generations were also evaluated for seedling reaction against the most avirulent leaf rust race 11. At seedling stage Chris and Egret have two dominant complimentary genes against race 11, while cultivars Banks has a dominant gene for race 11. In case of race 77A each of the three cultivars was ascribed to two dominant genes for leaf rust resistance. The expected presence of gene $Lr34$ in Chris, Egret and Banks were suggested as ideal stocks for use in breeding programme aimed at evolving durable leaf rust resistant varieties.

The experimental material of F$_2$ and F$_3$ generations of three crosses viz., WH 542 x Arkan, UP 2338 x Blueboy II and UP 2338 x Centurk was screened by Datta et al. (2004) at the seedling stage with pathotype 121 R 63-1 by growing with susceptible Agra Local in aluminum bread pan trays in artificial epiphytotic conditions. They reported that all the three exotic winter wheat cultivars viz., Arkan, Blueboy II and Centurk had one dominant brown rust resistant gene, $Lr24$ operating against the pathotype 121 R 63-1.

A synthetic hexaploid wheat (SHW) lines (Syn 419) developed through hybridization between *Triticum turgidum* and *Triticum tauschi* was crossed with Agra Local by Raza Haghparast et al. (2004) and F$_1$, F$_2$, F$_3$ and backcross generations alongwith their parents were screened at seedling and adult plant stages against the pathotype 77-5 (121 R 63-1).
They reported that partially dominant gene identified from Syn.419 might be a useful source of resistance to leaf rust.

Genetic basis of leaf rust resistance cultivars Dove developed at CIMMYT was studied by Kaur and Saini (2004) against Indian leaf rust race 77-5. The \( F_1 \), \( F_2 \) and \( F_3 \) generations from the cross Dove x WL 711 were sown in open experimental field and leaf rust was developed in the experimental area by artificial inoculation of race 77.5. The resistance at adult plant stage against 77-5 (the most virulent race from Indian subcontinent) was ascribed to two genes. One of these two genes is the non-hypersensitive adult plant resistance gene \( Lr34 \). The second gene is a new and as yet undescribed recessive hypersensitive adult plant resistance gene.

2.2 Genetics for grain yield and filling period related traits

The appropriate literature pertaining to present studies on genetics for related traits of grain yield and filling period in wheat and some important relevant studies in other cereals have been reviewed as under.

2.2.1 Heterosis and inbreeding depression

Mani and Rao (1975) studied 55 crosses involving the crossing of eight winter and three spring exotic varieties with five Indian high yielding cultivars of different heights. The mid parent heterosis to the extent of 193% was observed for grain yield in the winter x spring wheat cross, V 35 x Sharbati Sonara. Only few crosses showed significant
values of heterosis for number of tillers per plant, number of grains per ear, weight of grains per ear and 100-grain weight.

While studying six wheat crosses, Singh and Singh (1978) reported that relative heterosis ranged from 30.55 per cent for effective tiller number to 76.85 per cent for grain yield per plant. The hybrids showing higher heterosis also showed high inbreeding depression. The crosses Norteno 67 x Moti and Kalyan Sona x Norteno 67 had 38.61 per cent and 8.4 per cent heterosis but only 3.69 per cent and 1.69 per cent inbreeding depression for yield and grains per spike respectively. The increase in vigour of the F5 in such cases was expected to be mainly due to accumulation of favourable additive genes and complementary effects both being fixable. Such crosses are expected to throw desirable segregants which may be handled through pedigree method and suitable varieties may be released.

Twelve lines, five tester and resulting 60 crosses were evaluated by Rajore (1999) to derive information on heterosis for grain yield and its components in wheat. He observed positive and significant heterobeltiosis in 26 crosses for grain yield per plant, 17 crosses for grains per spike, 23 crosses for 1000-grain weight and 13 crosses for harvest index.

Nehvi et al. (2000) studied hybrids involving 10 lines and three morpho-physiologically diverse testers in wheat. Significant heterosis for
number of tillers per plant, number of grains per ear, 1000-grain weight and grain yield per plant was observed. The cross S 56 x IID 2380 exhibited significantly the highest heterosis over both the parents for grain yield per plant.

Sharma et al. (2002) estimated heterosis over mid and better parent and inbreeding depression in 10 x 10 diallel set in durum wheat. Marked better parent heterosis for grain yield (up to 68.8%) and its important components was observed. The heterobeltiosis ranged from 9.2 to 12.3% for spike length, -10.5 to 8.3% for spikelets per spike, -23.7 to 20.1% for number of grains per spike and -11.8 to 27.5% for 1000-grain weight.

Heterosis and inbreeding depression of grain yield and its components was estimated by Rathod (2003) using generation mean analysis in six crosses of bread wheat. He observed that the most of the crosses exhibited significant heterosis, heterobeltiosis and inbreeding depression for the characters like number of tillers per plant, plant height, flag leaf area, length of main spike, number of spikelets, grains per spike, grain yield per plant and harvest index. In case of days to flowering and grain protein content, a poor heterobeltiosis was observed.

Singh and Singh (2003) studied heterosis in the 8 x 8 diallel set of wheat. They reported that the magnitude of heterosis was the highest (74.4 %) for grain yield over better parent and for total dry matter
(72.3 %) over standard variety. The high magnitude (52.6 %) of standard heterosis was observed for grain yield.

Tariq et al. (2004) evaluated 10 spring wheat cultivars and their 30 F₁ hybrids to estimate mid-parent heterosis for yield and yield related traits. The mid-parent heterosis ranged from –24.5 to 107.9% for tillers per plant –10.9 to 16.5% for spike length, -13.7 to 7.9% for spikelets per spike, -33.6 to 17.1% for kernels per spike, -21.7 to 61.6% for 1000-kernel weight and –55.7 to 156.8% for grain yield per plant.

A study was conducted with 10 parents diallel by Singh et al. (2004) in bread wheat under three different environments. Marked heterobeltiosis for grain yield and its important components was observed. A total of 20 crosses showed significant consistent heterobeltiosis for grain yield per plant over all the three environments. The maximum heterobeltiosis for grain yield per plant was 50.94% (Raj 3765 x HD 2285), 121.08% (PBW 373 x HD 2329) and 93.96% (PBW 373 x HD 2329) in both early and normal plantings. The crosses showing heterosis for grain yield were not heterotic for all the characters. Heterosis for grain yield per spike followed by tillers per plant and 1000-grain weight was independently associated with heterosis for grain yield in early and normal plantings. However, heterosis for grain yield per spike, dwarf plant height and tillers per plant contributed maximum towards yield heterosis. Significant inbreeding depression was recorded
frequently for yield and yield contributing traits. However, in a few traits, it was observed significant negative, indicating that F$_2$ was superior to F$_1$ generation.

2.2.2 Gene effects

The parental, F$_1$ and backcross generations of two winter wheat crosses were studied by Edward et al. (1976). They stated that only additive gene effects were involved for plant height, number of tillers per unit area and kernel weight. While heading date was controlled by genes with additive and dominance effects. They suggested that selection in early segregating generation should be effective for plant height, tiller number and kernel weight. On the other hand, conventional selection for early heading should be delayed to later generations for a more tangible advance.

Randhawa and Minhas (1977) studied a set of diallel cross involving five wheat genotypes. Positive overall heterosis was observed for all the characters except 100-grain weight. The results indicated that both gca and sca variance were significant for all the characters except number of spikes per plant. The additive effects were predominant in general, however, dominance or over dominance effects were equally important for grain yield.

The P$_1$, P$_2$, F$_1$, F$_2$, BC$_1$ and BC$_2$ generations of twenty eight wheat crosses were studied by Chatrath et al. (1986) to know the nature and
magnitude of gene action for grain yield. They found that additive and additive x additive gene effects were important in the control of yielding ability. They concluded that improvement in yield could be achieved through progeny selection, which exploits additive and additive x additive effects.

Sharma *et al.* (1986) evaluated six generations *viz.* $P_1$, $P_2$, $F_1$, $F_2$, $BC_1$ and $BC_2$ of two crosses in wheat. Additive as well as dominance gene effects governed the inheritance of grain weight per spike but the additive gene effects were greater than dominance. However, dominance with duplicate types of epitasis was observed for the inheritance of grain yield. They concluded that attempts for progeny testing and the selection in early segregating generations would be advantageous for genetic improvement of the present material.

Using means of the $P_1$, $P_2$, $F_1$, $F_2$, $BC_1$ and $BC_2$ generations, Singh and Rai (1987) estimated gene effects governing different traits in wheat and reported that dominance component was positive and highly significant in all the crosses for all the traits except spike length. The additive components was also present in sizable proportion. The four out of ten crosses studied showed high mean performance for yield and yield related traits and exhibited the presence of dominance and sizable amount of additive component of genetic variances. These crosses should be utilized in wheat improvement programme.
Pawar et al. (1988) estimated gene effects through generation means analysis for six yield related traits in four crosses of wheat. The best fitting model was applied in each case by excluding the non-significant parameter(s). The dominance gene effects were more important than additive gene effects in almost all cases, which showed presence of both kind of gene effects. Presence of trigenic or higher order interactions or linked digenics was indicated for tillers per plant and grain yield per plant in cross HD 2122 x Sonalika. Epistasis played important role in the control of plant height, tillers per plant and grain yield per plant. While in case of 100-grain weight only additive gene effects were significant. These results indicated that improvement in grain yield per plant through indirect selection for grain weight would be more successful than through direct selection for grain yield itself.

An investigation was carried out by Singh and Singh (1992) using generation mean analysis for grain yield and related traits in 28 crosses of wheat. Additive gene effects were important in the inheritance of number of grains per spike and 100-grain weight. However significance of dominance gene effects for grain weight of 3 spikes and yield per plant were observed. Among the epistasis effects, additive x additive interaction was of considerable importance for all the characters, except 100-grain weight, for which additive x dominance was more important. They suggested that attempts should be made for progeny selection in
early segregating generations to exploit additive and additive x additive effects in the present material.

Five yield related components in six generations i.e. $P_1$, $P_2$, $F_1$, $F_2$, $BC_1$ and $BC_2$ of two wheat crosses (HD 2009 x Sonalika and Kalyan Sona x Sonalika) were studied by Srivastava et al. (1992) and reported that additive gene effects were predominant for all the traits, although non-additive gene effects were also important. Intermating followed by selection would provide better opportunities for isolating elite genotypes in wheat.

The $P_1$, $P_2$, $F_1$, $F_2$, $BC_1$ and $BC_2$ involving semi dwarf, dwarf and tall wheat cultivars were studied by Amawate and Behl (1995). The $F_1$s exceeded the better parent for grain yield per plant in cross Kalyan Sona x K 65 and UP 301 x K 65. Absence of epistasis was noticed in the cross Kalyan Sona x K 65, HD 2122 x K 65 and UP 301 x K 65 for grain yield per plant. Additive gene effects were observed for plant height and grains per ear in the cross HD 2122 x K 65 and for grain weight per ear in UP 301 x Hyb 65. Plant height and grain weight per ear were governed by additive x additive gene action in UP 301 x Hyb 65, while their expression were due to dominance x dominance gene interaction in other crosses. Thus importance of additive and additive x additive gene effects for plant height, grains per ear and 1000-grain weight, suggested improvement in these characters through selection.
Sharma et al. (1996) studied the parents, F1, F2, BC1 and BC2 generations of three crosses in wheat. The results indicated that additive gene effects were significant for grains per ear in all the crosses. The dominance effects were significant and higher in magnitude than the additive effects for days to flowering in CPAN 1961 x MOW 27 and Eagle x Mendose cross, for tillers per plant and plant height in CPAN 1961 x HUW 27 cross and for grain weight per ear in Eagle x Mendose cross. Both fixable and non-fixable gene effects were significant for tiller per plant in CPAN 1933 x HW 517 and Eagle Mendose, for plant height and biological yield in Eagle x Mendose and for grain yield in CPAN 1961 x MUW 27. The situation, where both additive and non-additive gene effects were important, biparental mating followed by selection should be adopted for improving such traits.

Yadav et al. (1997) studied the inheritance of tillers per plant, grains per ear 1000-grain weight and grain yield per plant in two wheat crosses (WH 280 x WH 283 and WH 291 x NP 846). Genes controlling tillers per plant were dominant in WH 280 x WH 283 and recessive in WH 291 x NP 846. Whereas, genes controlling grains per ear showed no dominance in both the crosses. Grain yield per plant was partially dominant in WH 280 x WH 283 and completely dominant in WH 291 x NP 846. Additive gene effects were predominant for grains per ear, in which simple selection procedures could be used efficiently. However,
presence of dominance and epistasis effects for most of the traits in both the crosses would slow down the progress. In such a situation, for exploitation of additive, dominance and epistasis gene effects simultaneously and breaking of undesirable linkages, intermating among potentially desirable plants in early segregating generations would be advantageous.

Six generations viz., P₁, P₂, F₁, F₂, BC₁ and BC₂ of 19 crosses involving 20 diverse wheat genotypes were studied by Singh et al. (1998) for grains per spike, 1000-grain weight and grains per spikelet. Additive and additive x additive gene effects were significant in majority of the crosses. The magnitude of additive gene effects was smaller compared to other gene effects. Dominance and dominance x dominance gene effects were of a large magnitude and present in 33 per cent of the crosses, but could be unexploited due to the presence of duplicate epistasis. Detection of both fixable and non-fixable gene actions and duplicate epistasis indicated that improvement in these yield components would not be possible by simple selection procedures. The use of biparental approach or intermating in early segregating generation followed by selection would be effective.

Chand (1999) evaluated six generations i.e. P₁, P₂, F₁, F₂, BC₁ and BC₂ of three crosses in bread wheat. Both additive and dominance gene effects were significant for 1000-grain weight and grains per ear in all the
crosses, grain yield per plant and spikelets per ear in CPAN 1866 x HD 2009 cross and plant height in CPAN 1866 x DL 153-2 cross. The dominance gene effects were significant for grain yield and spikelets per ear in CPAN 1886 x DL 153-2 and grain weight per ear in CPAN 1866 x HD 2009 and CPAN 1866 x DL 153-2. Biparental mating or selective diallel mating system would be useful for improvement in these traits.

Six generations (P₁, P₂, F₁, F₂, BC₁ and BC₂) of two crosses (WH 151 x WH 147 and Sonalika x CPAN 1444) were studied by Mehla et al. (2000) to ascertain the information on nature and magnitude of gene actions for grain yield and other related quantitative traits in spring wheat. Dominance gene effects and additive x additive interactions were involved in the inheritance of days to heading, spike length and spikelets per spike. However, for biological yield, grain yield and harvest index the additive x additive and dominance x dominance interactions were important. They suggested that reciprocal recurrent selections should be followed which exploit both additive and non-additive gene actions for these traits.

The P₁, P₂, F₁, F₂, BC₁ and BC₂ generations of four crosses in durum wheat were studied by Dhillon et al. (2002) for grain yield per plant, grains per spike, effective tillers per plant and 1000-grain weight. Additive and additive x additive effects were observed for yield and yield
components, which could be exploited following pedigree method of selection.

Ved Prakash and Joshi (2003) studied the parents, $F_1$, $F_2$, $BC_1$ and $BC_2$ generations of two wheat crosses under normal and late shown conditions. Both additive and dominance gene actions influenced the expression of the characters studied, however relative magnitudes of dominance were higher than additive under both the environments. Additive x additive and dominance x dominance interactions were generally important for the expression of all the traits under both environments. Desirable significant heterosis was observed for plant height, grains per spike and grain yield per spike. They suggested that biparental mating or selective diallel mating might be helpful for improvement in the traits studied.

Joshi et al. (2004) studied half diallel set of 45$F_1$s and 45$F_2$s involving ten genetically diverse varieties of hexaploid wheat. The variance due to gca and sca were highly significant for all the traits studied in both $F_1$ and $F_2$ generations. However the gca : sca ratio indicated preponderance of additive gene effects for $F_1$ and $F_2$ generation for all the characters, except 100-grain weight, in which non-additive gene effects were predominant.

Kaur and Singh (2004) studied six generations namely, $P_1$, $P_2$, $F_1$, $F_2$, $BC_1$ and $BC_2$ of three wheat crosses. Additive gene effects were
significant in all the crosses for all the traits except effective tillers per plant in CHM 74.540 x PDW 274 and CHM 74.540 x PDW 277. The nature and magnitude of gene effects vary with different crosses and characters, thus they opined that specific breeding strategy should have to be adopted for particular cross to get improvement.

### 2.2.3 Heritability and genetic advance

Shang et al. (1982) estimated heritability in F$_2$ progenies of crosses between seven bread wheat parents and reported high broad sense heritability for days to heading (70 – 94 %) and moderate for harvest index (58–64 %). Additive effects were observed for above mentioned two characters.

Camargo and Oliveira (1983) crossed IACS 5 of normal height with the semi dwarf Siete Cerros and the dwarf varieties Tordo, Vican 71 and Olesen. Data on yield, height and several yield components were recorded in the parents, F$_1$ and F$_2$ populations and reciprocal back crosses. They obtained 0.878 estimate of broad sense heritability for plant height. This estimate was around 0.5 for 100-grain weight and number of spikelets per ear and number of ear per plant. Yield and other components exhibited heritability estimates less than 0.4. They further found that additive effect was the main source of inheritance in all the characters except 100-grain weight.
A field experiment was conducted by Khan et al. (1987) to assess heritability and genetic advance in ten F$_2$ of bread wheat. Moderate to high heritability with moderate genetic advance under selection was observed for days to heading, plant height, number of ear per plant, grains per ear and 1000-grain weight.

Pawar et al. (1988) obtained information on estimates of heritability and genetic advance by using F$_2$ population of ten bread wheat crosses. Highest value of heritability for grain yield per plant, plant height, days to flowering, number of spikelets per ear, 1000-grain weight, number of grains per ear indicated that these traits mostly under genetic control. High values of both heritability and advances for grain yield per plant, tillers per plant and plant height indicated the role of additive gene effect in the inheritance of these characters.

Thakur et al. (1989) recorded observation on seven yield component characters and grain yield in ten parents along with their eleven F$_2$ crosses. Tiller numbers per plant and grain yield possessed high heritability coupled with high genetic advance, which is indicative of contribution of additive genetic variation in the expression of both these traits.

Bajendrapal and Garg (1992) studied parental, F$_1$ and F$_2$ generations of three wheat crosses. Results revealed that heritability and genetic advance were high for grain yield and number of tillers per plant,
grain per ear and biological yield. The Cross CPAN 1962 x CC 493 was in general superior to the others for heritability and genetic advance for most of the traits.

Information on heritability was derived by Yadav and Mishra (1992) from data on seven yield components in 25 $F_2$ populations grown under high and low fertility conditions. High heritability was observed in the material sown under high fertility conditions while 100-grain weight, grain yield per plant and grains per ear exhibited high estimates of heritability in low fertility condition.

Khairalla (1993) estimated heritability for grain yield and five yield components in $F_3$ generation of a cross between cultivars Giza 155 and West Bred (USA). He found that broad sense heritability was high for spike length, grains per spike and 1000-grain weight, but moderate for spikes per plant and grain yield per plant.

Fantini et al. (1994) studied parental, $F_1$, $F_2$, $BC_1$ and $BC_2$ generation in 14 crosses of bread wheat for the important agronomic characters. High heritability along with high genetic gain was recorded for flag leaf area, grains weight per spike, grain yield per plant, biological yield per plant and harvest index.

Variability parameters were computed by Kumar and Luthra (1995) using $P_1$, $P_2$, $F_1$, $F_2$, $F_3$, $BC_1$, $BC_2$, $BC_1S$ and $BC_2S$ generations of two bread wheat crosses i.e. HD 2329 x Kalyan Sona and HD 2009 x
Sonalika. Peduncle length showed the highest heritability in cross HD 2329 x Kalyan Sona whereas harvest index exhibited the highest heritability in cross HD 2009 x Sonalika. Spike number and 1000-grain weight showed the lowest heritability in crosses HD 2329 x Kalyan Sona and HD 2009 x Sonalika, respectively. In this study, high heritability was associated with low genetic advance for yield per plant, spike number, number of grains per spike, days to ear emergence, flag leaf area, grain filling period, peduncle length, biological yield and harvest index in both the crosses. They further suggested that direct selection on yield per se would not be proper for further improvement of such population and due weightage may be given to different yield components.

Ozkan et al. (1997) observed transgressive segregation for number of grains per ear, grain weight per ear, biological yield per plant, grain yield per plant and harvest index per plant in $F_2$ population of cross involving Kauz “S” and 84 C2T 04 cultivars. High heritability combined with considerable genetic advance in the cross indicated that additive gene effects were important for these traits.

$F_2$ bread wheat populations developed from eight parental lines of diverse heritage were studied by Ansari et al. (1999) for broad sense heritability and genetic advance. $F_2$ hybrids and their parents differed significantly for all the traits $viz.$, number of tillers per plant, main spike length, number of spikelets per spike, number of grains per spike, 100-
seed weight and grain yield per plant indicating the existence of genetic variation among the genotypes. High heritability coupled with high genetic advance observed in most of the progenies for most of the traits indicated quantitative pattern of inheritance offering better chances of selection for the traits. The cross Sarsabz x Mehran-89 showed significantly highest grain yield (39.48 g) and 100-seed weight (6.73 g) with considerable heritability (76.59% and 74.21% respectively) and low genetic advance probably due to non-additive gene effects. The cross Pak-70 x Sarsabz displayed maximum heritability (96.48%) associated with the highest genetic advance (42.69) for 100-seed weight indicating the involvement of additive gene action.

A study was conducted by Satyavart et al. (2002) to estimate the heritability for yield and its ten components in bread wheat using seven generation (P₁, P₂, F₁, F₂, F₃, BC₁ and BC₂) of cross C 306 x S 948. Heritability was maximum for ear length followed by number of grains per ear and peduncle length, whereas genetic advance was higher for plant height, peduncle length and ear length.

Khan et al. (2003) studied the F₂ population of six cross combinations involving six wheat cultivars/lines. The broad-sense heritability values for plant height and number of tillers per plant was ranged from 49.83 to 88.83 and 52.25 to 88.82 per cent, respectively. These heritability estimates ranged from 66.31 to 85.01 and 47.72 to
84.59 per cent for flag leaf area and peduncle length, respectively. The broad-sense heritability for grain yield per plant ranged from 65.58 to 90.01 per cent. The genetic advance values for plant height, number of tillers per plant, flag leaf area, peduncle length and grain yield per plant ranged from 6.30 to 19.88, 1.87 to 4.42, 4.78 to 10.10, 2.68 to 10.38 and 4.95 to 11.61, respectively. The cross WLRG 3 x 5039 appeared to be the most promising for the selection of high yielding wheat genotypes.

Khan and Khan (2004) estimated broad sense heritability and genetic advance in F$_2$ populations of bread wheat developed from 15 diverse lines. Parents and F$_2$ were differed significantly for all the traits viz., number of tillers per plant, spike length, number of spikelets per spike, number of grains per spike, 1000-seed weight and grain yield per plant indicating the existence of genetic variation among the genotypes. High heritability coupled with high genetic advance observed in most of the progenies for spike length, grain yield per plant showed the quantitative pattern of inheritance were governed by additive gene action and offering better chances of selection for these traits.

2.2.4 Correlations

The association study was carried out by Rasmusson et al. (1979) in five population obtained from intercrossing among nine barley cultivars. They reported that proportion of days in grain filling was negatively correlated with number of days in the vegetative period and
positively correlated with days in the grain filling period. Vegetative period was negatively correlated with grain filling period in four of five populations, but the values were relatively small chiefly influenced by non-additive gene effects.

Yadav and Murthy (1979) made crosses of single, double and triple semi dwarf with tall wheat in an 8 X 8 diallel mating design. They noted that among six yield components, a number of significant correlation found in F₁ were broken in F₂ due to recombination and certain unbroken correlations could be weakened or overcome in biparental progenies. They reported that grain yield per plant exhibited significant correlation with ear per plant, spikelets per ear and 100-grain weight. They suggested that 100-grain weight could be improved in semi dwarf wheat through repeated cycles of biparental mating of divergent parents F₂ and its subsequent generations.

Nanda et al. (1980) evaluated F₂, biparental and F₃ generations of WG 357 X Tobari 66 in bread wheat and reported that grain yield was positively correlated with tiller number, grain size, grain number per ear, spikelets per spike and ear length but not with heading date in F₂ and biparental, nor with plant height in F₂ generations. The magnitude of correlation coefficient varied over generations and the magnitude of genotypic and phenotypic correlation was not comparable. They suggested that correlation must be tested over generations.
Sixteen cultivars of wheat were studied by Gebeyehou et al. (1982). They observed that the length of grain filling period was significantly and positively correlated with kernel per spike ($r = 0.39^*$), kernel weight ($r = 0.56^{**}$) and grain yield ($r = 0.39^*$). Positive correlation was also revealed between the length of vegetative period and these three characters but was only significant with kernel weight ($r = 0.42^{**}$).

Association among five characters was investigated by Falcineili et al. (1983) in $F_2$, $F_3$ and $F_4$ generations of five bread wheat crosses. They found significant and positive relationship for 1000-grain weight, days to heading and height between all three possible pair of generations. Height was significantly and positively correlated with 1000-grain weight, and days to heading was significantly and negatively associated with 1000-grain weight in all the three generations.

In $F_2$ generation of a 7-parental diallel (excluding reciprocals) in bread wheat, Singh et al. (1985) observed positive and significant relationship of grain yield with spikes per plants, plant height, spikelets per spike, grains per spike and 1000-grain weight. They also found significant and positive correlation between spike length and 1000-grain weight, spikelets per spike and grains per spike, spikelets per spike and spikes per plant, and 1000-grain weight and grains per spike.

Bruckner and Frohberg (1987) recorded rate and duration of grain filling in 20 genotypes of spring wheat growing in four rainfed
environments. They found that the rate but not duration of grain filling was correlated with grain weight. There was no association between rate and duration of grain filling. Results suggested that simultaneous selection for high grain filling rate and grain weight could be possible without increasing grain filling duration, while selection for high grain filling rate could be possible via selection for higher grain weight.

Knott and Gebeyehou (1987) studied three crosses of durum wheat for two years. They found that lengths of vegetative and grain filling period were negatively correlated with yield in both the years. Correlations between yield and length of vegetative growth and grain filling period were inconsistent. They suggested that if two characters are controlled by the same genetic system acting in the same direction in each case, they will show a positive correlation, but if controlled by separate genetic systems, they should not be correlated. They further pointed out that in case of late season drought, if a line had a long vegetative period, it could force to fill its kernels in a shorter period but for lines with short vegetative period, longer period may be available for kernel filling. The data provided no indication that there was an optimum combination of lengths of vegetative and grain filling period that resulted in maximum yields under the two years.

Khan et al. (1987) conducted field experiments involving 18 lines and their 10 F2 populations of bread wheat. Grain yield per plant was
positively correlated with number of ear per plant, ear length, grains per ear and 1000-grain weight while it was negatively associated with days to heading and days to maturity. Days to maturity showed negative correlation with 1000-grain weight which indicated the importance of heading to maturity period for longer grain size. In case of ears per plant, its correlation was positive with days to maturity and ear length, and negative with number grains per ear. The ear length showed strong correlation with grains per ear in positive manner.

From the study of yield correlation in F₂-F₄ generations from bread wheat crosses viz., Mironovskaya Yubileinaya x Graecum 114, FK 25 x Sval of 01320 and Lutescens 298-54 x Red River 68, Mikheev (1992) reported significant correlation between yield with ear length, number of spikelets, grains per ear and 1000-grain weight in all generations.

Tiwari and Rawat (1993) reported that grain yield per plant was significantly and positively correlated with plant height, ear length, number of tillers per plant, number of spikelets per spike, biological yield and number of ears per plant. They obtained above findings from the F₃ generation of bread wheat.

Korkut (1994) examined association of morphological traits under early and timely sown conditions in F₄ population. They reported that flag leaf area, peduncle length, spike length, grains per spike, 1000-grain weight, biomass per plant and harvest index correlated positively and
significantly with grain yield in both the sowing conditions. While grain yield was positively and significantly correlated with plant height in early sowing and with tillers per plant in timely sowing. In both sowing conditions days to heading negatively and significantly correlated with grain yield.

Dalal et al. (1995) estimated correlation coefficient among four traits in F$_3$ populations of two wheat crosses viz., WH 283 x WH 280 and NP 846 x WH 291. They found that tillers per plant and grains per spike had significant positive correlation with yield per plant in both crosses. While 1000-grain weight showed positive and significant association with yield per plant only in NP 846 x WH 291 cross. Relationship was significant but negative between harvest index and yield per plant in case of both the crosses (WH 283 x WH 280 and NP 846 x WH 291).

Kaushik et al. (1996) computed correlation coefficient in F$_2$ generation of two bread wheat crosses viz., WH 416 x UNC 1 and HSW 147 x Kalyan Sona. Tillers per plant, grains per ear and biological yield per plant had positive and significant correlation with grain yield per plant in both the crosses. Tillers per plant and grain yield per plant had also positive and significant association with biological yield per plant in F$_2$ population of WH 416 x UNC 1 cross. In case of HSW 147 x Kalyan Sona, positive and significant correlation was observed between grains per ear and biological yield per plant.
While studying the 23 segregating populations of bread wheat Nirala and Jha (1996) reported that three characters viz., days to maturity, tiller number per plant and effective tillers per plant were positively associated with grain yield per plant.

Study of character association was made by Tammam et al. (2000) using parents, F₁ and F₂ generations of five bread wheat genotypes in a half diallel cross. Grain yield per plant had a positive correlation in both magnitude with each of days to heading (in the parents and the F₂ generation), number of spike per plant, number of kernels per spike (in F₁ and only for genotypic level in the parents and the F₂ generation), 1000-kernels weight (in the parents and for genotypic correlation in the F₂ populations) and biological yield per plant in all generations. Number of kernels per spike showed significant negative phenotypic and genotypic correlation coefficients with 1000- kernels weight in the F₂ population and significant positive genotypic correlation with biological yield in all generations. Thousands kernel weight showed positive and significant relationship with all traits except biological yield at both the levels.

Esmail (2001) evaluated seven genetically diverse wheat parents, their F₁ and F₂ populations resulting from diallel cross to estimate the association of grain yield with related traits. Phenotypic and genotypic correlations between all possible pairs of traits studied were different in magnitudes when estimated from the parents, F₁ and F₂ generations. Grain yield per plant was positively correlated with number of spikes per plant,
plant height and days to heading but negatively correlated with grain weight per spike in the parents, $F_1$ and $F_2$ generations at the phenotypic and genotypic levels. The largest negative phenotypic and genotypic correlation was obtained between number of spikes per plant and grain weight per spike in the three populations.

Snecor (2001) studied segregating generation of wheat to know the genotypic correlation among grain yield and its related characters. He found that number of seeds per spike had the highest positive correlation with grain yield followed by 1000-grain weight and spike length. Days to 50% flowering showed highly significant negative correlation with seed yield. Hence, for improving grain yield in wheat, selection should largely depend upon early maturity, number of seeds per spike and spike length.

Dhayal et al. (2003) carried out the correlation analysis between yield and its components in parents, $F_1$ and $F_2$ generation of wheat under normal and salinity conditions. Under normal condition, plant height, number of productive tillers per plant, grain weight per ear and 1000 grain weight showed significant correlation with grain yield while under salinity only number of productive tillers per plant had significant positive association at genotypic and phenotypic levels. However, correlation coefficients were in general stronger at genotypic level in both the environments.
III. MATERIALS AND METHODS

The present investigation on "Genetics for slow-rusting and yield related traits in bread wheat (Triticum aestivum L.Em. Thell.)" was carried out at the Wheat Research Station, Junagadh Agricultural University, Junagadh under irrigated conditions in *rabi* 2004. Geographically, Junagadh is situated at 21.5° N latitude and 70° E longitude with an altitude of 60 meters above the mean sea level. The soil of the region is medium black, alluvial in origin and poor in organic matter. The climate of the area represents the tropical condition with semi-arid nature. There is a short winter available for wheat crop in this region.

3.1 Selection of experimental material

The experimental material was comprised of four crosses each with six basic generations, *viz.*, P₁, P₂, F₁, F₂, BC₁ and BC₂ five parents involving in these crosses were selected from genetic stocks available at the Wheat Research Station, JAU, Junagadh based on leaf rust reaction data recorded during *rabi* 2001. The details of selected parents are given in Table 3.1. Among the genotypes used, J 24, Lok 1 and Kalyan Sona are released varieties in Gujarat and are now susceptible to leaf rust, whereas, HD 2189 and HS 347 are promising lines and resistant to leaf rust.
Table 3.1 The details of parents selected for present study

<table>
<thead>
<tr>
<th>Sr No</th>
<th>Genotype</th>
<th>Pedigree</th>
<th>Reaction to leaf rust</th>
<th>Origin</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>HD 2189</td>
<td>HD 1963/HD 1931</td>
<td>Resistant</td>
<td>IARI, New Delhi</td>
</tr>
<tr>
<td>2</td>
<td>HS 347</td>
<td>BAU&quot;S&quot;</td>
<td>Resistant</td>
<td>Shimla, (Himachal Pradesh)</td>
</tr>
<tr>
<td>3</td>
<td>J 24</td>
<td>S 306/WS 217</td>
<td>Susceptible</td>
<td>Junagadh (Gujarat)</td>
</tr>
<tr>
<td>4</td>
<td>Kalyan Sona</td>
<td>(Fₙk55/HtbNio) GB55</td>
<td>Susceptible</td>
<td>Ludhiana (Punjab)</td>
</tr>
<tr>
<td>5</td>
<td>Lok 1</td>
<td>S 308/S 391</td>
<td>Susceptible</td>
<td>Lok Bharati Sanosara (Gujarat)</td>
</tr>
</tbody>
</table>

3.2 Crossing programme

J 24 x HD 2189 (Cross 1), J 24 x HS 347 (Cross 2), Lok 1 x HD 2189 (Cross 3) and Kalyan Sona x HS 347 (Cross 4) hereafter referred to as Cross 1, Cross 2, Cross 3 and Cross 4, respectively, were made between susceptible and resistant parents in rabi 2002. Four F₁s along with their five parents were grown in the rabi 2003 to obtain BC₁ and BC₂ generations. F₂ generation was developed by selfing the F₁ plants. For making crosses, i.e. fresh crosses and backcrosses, sufficient number of female plants were emasculated. Emasculation was done in the evening 16.00 to 18.00 hrs. The spikes likely to undergo anthesis in next day morning were selected. Some upper and lower spikelets in a spike
were removed. One-third portion of spikelets along with awn was cut by scissors. All the three anthers from each spikelet were removed with the help of forceps. Emasculated spikes were then covered with butter paper bags. Next day morning, pollens collected from the desirable male parent was dusted on emasculated spikes to effect pollination. F$_2$ generation was obtained by selfing the F$_1$ plants. Selfed as well as crossed seeds were collected at the time of maturity.

3.3 **Experimental design**

The experiment was laid out in compact family block design with three replications. Each replication was divided into four compact blocks each consists of single cross and blocks were consisted of six plots comprised of six basic generations of each cross. The crosses were assigned to each block and six generations of a cross were relegated to individual plot within the block. The single plot of one row for each parent and F$_1$, two rows for each back cross and five rows for each F$_2$ generation where sown during *rabi* 2004. The rows of 2.5 meter length spaced 22.5 cm apart keeping 10 cm distance between two plants within the row.

Infector (Agra Local) rows surrounding and within the experiment were provided to ensure uniform inoculums load of brown rust. Two infector rows parallel to each replication along with two rows on each of
the other sides were sown. Besides this, one row of infector after every three rows within the replications was grown.

The experimental area was fertilized with 120 kg ha\(^{-1}\) N and 60 kg ha\(^{-1}\) P in the form of urea and diammonium phosphate, respectively. One half quantity of N and total amount of P was applied in the soil before sowing and remaining one half quantity of N was top dressed at 18 days after sowing.

The experiment was sown in dry soil conditions at normal sowing time and irrigated on the same date. Second irrigation was given six days after sowing for better germination and good seedling growth. The crop was irrigated third time 18 days after sowing, i.e., at crown root initiation stage and then after, irrigation was applied regularly at one week interval until attained grain maturity. A total of 15 irrigation were required to harvest the crop. Pendimethalin (2.5 kg @ ha\(^{-1}\)) was applied as pre-emergence for weed control by spraying on soil surface after 48 hrs of giving first irrigation. Other cultured practices in vogue were followed for reaping better crop.

3.4 Raising of leaf rust nursery

To have sufficient quantity of inoculums, separate wheat leaf rust nursery (cultivar Agra Local) was sown one month before the regular sowing of experiment. Initial stalk of a mixture of prevailing races of *Pucinia triticina* Eriks (77-2, 77-5, 77-3, 77A, 104, 104-2, 104-3, 12-2
and 162) received from Directorate of Wheat Research, Regional Station, Flowerdale, Shimla was used for the multiplication of inoculums. About 15 days old seedlings (two to three leaf stage) were used for first inoculation. Leaves of selected seedlings were dewaxed with wet fingers and uredospore mixed chalk powder was rubbed on leaf with the help of fingers. Inoculation was performed at evening time. Additional water was atomized onto the entire group of inoculated plants to provide the moist condition. A clear polyethylene sheet was placed over the wooden frame of wet muslin sheet to enclose the plants completely. This arrangement provided high humidity and kept the leaves wet until next morning when the chamber was disassembled around 9.00 hrs. Sufficient inoculum was produced in the nursery, which was further used to create epiphytotic conditions artificially in the experiment.

3.5 Artificial inoculation of rust

To allow sufficient infection of rust to occur in the experiment, artificial inoculations were made at seedling stage in every spreader (infector) row. Upper side second or third leaf of 15 days old seedling was dewaxed with mixture of uredospores and chalk powder. At the same day, field was irrigated at late afternoon to provide sufficient humidity. In addition, fresh ureadospores collected from rust nursery were suspended in water with three drops of the surfactant Tween 20 and sprayed in experimental field. Same practices were done second time at
10 days after the first inoculation. The leaf rust was allowed to build up within the plots by secondary infection.

3.6 Characters studied

The observations were recorded on five plants from P₁, P₂ and F₁, twenty plants from BC₁ and BC₂ and fifty plants from F₂ generations in each replication. Plants were selected at random from each plot and tagged before the ear emergence. The method/technique used for data collection on individual character is described below.

A. SLOW LEAF-RUSTING

Leaf rust infection per cent (AUDPC): Leaf rust intensities based on the modified Cobb’s scale for cereal rust (Peterson et al. 1948) were recorded for individual plants at five different dates starting from 2\(^{nd}\) February to 2\(^{nd}\) March, 2005 with an interval of seven days (i.e. 2\(^{nd}\), 9\(^{th}\), 16\(^{th}\), 23\(^{rd}\) February and 2\(^{nd}\) March.). The data collection were started when most of the plants reach to boot stage and continued up to the most of the plants attained physiological maturity. The area under the disease progress curve (AUDPC) was determined for each plant using the following formulae suggested by Peterson et al. (1948).

\[
\text{AUDPC} = \sum_{i=1}^{n-1} \left[ \frac{(x_i+x_{i+1})}{2} \right] (t_{i+1} - t_i)
\]
Where,

\[ \sum = \text{summation}, \]
\[ x_i = \text{leaf rust severity on } i^{\text{th}} \text{ date}, \]
\[ x_{i+1} = \text{Leaf rust severity on next date of observation}, \]
\[ t_i = i^{\text{th}} \text{ day of observation}, \]
\[ t_{i+1} = \text{interval in days between } i^{\text{th}} \text{ day to next date}, \]
\[ n = \text{number of days on which disease was recorded}. \]

The AUDC value of individual plant measures the intensity as well as the rate of the disease increase and represents the relative slow-rusting characteristics of a genotype.

B  GRAIN YIELD AND FILLING PERIOD RELATED TRAITS

1. **Days to ear emergence:** This was determined on individual plant basis as days from date of sowing to the date on which the tip of upper most spikelets of main ear emerged beyond the auricles of flag leaf.

2. **Days to maturity:** Days were calculated from date of sowing to the date of which selected individual plant attained physiological maturity. Physiological maturity was judged when approximately 75 per cent of glumes of primary spikes turned yellow.

3. **Vegetative period:** The date of anthers extrusion in the central florets of the main spike in selected plants was judged as date of
anthesis and duration in days from planting to anthesis was calculated as vegetative period.

4. **Grain filling period**: Days required from anthesis to physiological maturity were determined for each selected plant.

5. **Leaves per plant**: Green leaves on individual plants were counted at anthesis stage.

6. **Plant height (cm)**: The length of selected plants from ground level to the tip of main spike was measured in centimeter at maturity time.

7. **100 grain weight (g)**: Hundred kernels from individual plant produce were counted and weighed in grams on electronic balance.

8. **Grain yield per plant (g)**: Grains threshed from individual plant were dried, cleaned and weighed in grams on electronic balance.

### 3.7 Statistical analysis

3.7.1 **Analysis of variance**

The data collected on randomly selected five plants of parents and F₁, 20 plants of BC₁ and BC₂ and 50 plants of F₂ generation for individual characters were averaged and average values were subjected to statistical analysis according to compact family block design (Panse and Sukhatme, 1967). The analysis was carried out in two stages by taking crosses as families and different generations as progenies.
The structure of ANOVA for families is given in Table 3.2.

Table 3.2 Analysis of variance when a crosses (families) were raised in compact family block design with

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>MS</th>
<th>Expected mean squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Replication</td>
<td>(r-1)</td>
<td>( M_1 )</td>
<td>( \sigma^2e_1 + \sigma^2r )</td>
</tr>
<tr>
<td>Families</td>
<td>(f-1)</td>
<td>( M_2 )</td>
<td>( \sigma^2e_1 + \sigma^2f )</td>
</tr>
<tr>
<td>Error</td>
<td>(r-1) (f-1)</td>
<td>( M_3 )</td>
<td>( \sigma^2e_1 )</td>
</tr>
</tbody>
</table>

The analysis for the progenies under each family was done separately for each character. The form of analysis of variance for progenies was constructed as shown in Table 3.3.

Table 3.3 Analysis of variance of progenies within the family raised in compact family block design with

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>MS</th>
<th>Expected mean squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Replication</td>
<td>(r-1)</td>
<td>( M_4 )</td>
<td>( \sigma^2e_2 + p\sigma^2r )</td>
</tr>
<tr>
<td>Progenies within families</td>
<td>(p-1)</td>
<td>( M_5 )</td>
<td>( \sigma^2e_2 + r\sigma^2p )</td>
</tr>
<tr>
<td>Error</td>
<td>(r-1) (p-1)</td>
<td>( M_6 )</td>
<td>( \sigma^2e_2 )</td>
</tr>
</tbody>
</table>

Where,

\[ r = \text{number of replication}, \]
\[ f = \text{number of families}, \]
\[ p = \text{number of progenies within each family} \]
Before making comparison, a test of homogeneity of error variance for progenies was carried out for each character by applying Bartlett’s test of homogeneity as described by Panse and Sukhatme (1967).

From the Table 3.3, the following statistics were computed

1. Standard error of mean (SEm) = $\sqrt{\frac{M_6}{r}}$

2. Critical difference (CD) = SEm x $\sqrt{2} \times t_{(0.05)}$ at error degree of freedom

3. Coefficient of variation (CV %) = $\frac{\sqrt{M_6}}{\bar{X}} \times 100$

Where,

$M_6$ = error mean squares for progenies,

$\bar{X}$ = mean over progenies within the family

3.7.2 Generation means analysis

The standard statistical procedures were used to calculate means and variances of each generation for each character (Singh and Chaudhary, 1985).

$$\text{Mean (} \bar{X} \text{)} = \frac{\sum_{i} x_i}{N}$$
Variance for each generation was calculated separately to get variance of that generation. For example, variance of $P_1$ in replication was calculated as

$$\text{Variance of } P_1 = \frac{1}{N-1} \left[ \sum x_i^2 - \left( \frac{\sum x_i}{N} \right)^2 \right]$$

Variance of mean $(V_{p_1}) = \frac{(V_{p_1})^2}{N}$

Standard error $(SE_{p_1}) = \sqrt{V_{p_1}}$

Where,

$N$ = total number of observations

**Scaling tests**

Mather (1949) constructed scaling test, i.e. A, B and C (Table 3.4) to test the adequacy of simple additive dominance model and to detect presence of epistatic interaction. The significance of either of tests would indicate failure of simple additive dominance model to explain variation in generation means.
Table 3.4 Scaling tests and their expectations in absence and presence of non-allelic interactions.

<table>
<thead>
<tr>
<th>Scaling test</th>
<th>Expectation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Absence of non-allelic interactions</td>
</tr>
<tr>
<td>$A = 2BC_1 - F_1 - P_1$</td>
<td>0</td>
</tr>
<tr>
<td>$B = 2BC_2 - F_1 - P_2$</td>
<td>0</td>
</tr>
<tr>
<td>$C = 4F_2 - 2F_1 - P_1 - P_2$</td>
<td>0</td>
</tr>
</tbody>
</table>

The variances and standard errors of scaling test were calculated as under

Thus,

$$V_A = 4V_{BC_1} + V_{F_1} + V_{P_1}$$
$$SE(A) = \sqrt{V_A}$$

$$V_B = 4V_{BC_2} + V_{F_1} + V_{P_2}$$
$$SE(B) = \sqrt{V_B}$$

$$V_C = 16V_{F_2} + 4V_{F_1} + V_{P_1} + V_{P_2}$$
$$SE(C) = \sqrt{V_C}$$

The testing of individual scaling test was carried out by usual t-test. The degree of freedom for t-test was equal to the sum of degree of freedom for all type of generations involved in a particular scaling test and the degree of freedom of a particular generations was the total number of observations of that generation minus one.
Estimation of components of mean

The weighted least squares procedure as originally given by Cavalli (1952) and described by Mather and Jinks (1982) was followed to estimate the parameters of generation means. As six generations available in the present study, six equations were calculated for estimating the parameters \( m, (d) \) and \( (h) \). These were obtained by equating the observed generation means to their exceptions given in Table 3.5 for three parameters.

Table 3.5 Expectations of generation means for additive-dominance and digenic interaction model.

<table>
<thead>
<tr>
<th>Generation means</th>
<th>Additive-dominance model</th>
<th>Digenic interaction model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>m</td>
<td>(d)</td>
</tr>
<tr>
<td>( P_1 )</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>( P_2 )</td>
<td>1</td>
<td>-1</td>
</tr>
<tr>
<td>( F_1 )</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>( F_2 )</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>( BC_1 )</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>( BC_2 )</td>
<td>1</td>
<td>-0.5</td>
</tr>
</tbody>
</table>

These six equations were weighted with appropriate weights (reciprocal of variance of means) to obtained three normal equations to calculate three parameters. The three simultaneous equations were then solved by way of matrix inversion by adopting the following general
approach proposed by Cavalli (1952). This procedure was adopted for all
model-fitting components.

\[ M = J^{-1} S \]

Where,

\( M \) = column vector of the estimates of the
parameters,

\( S \) = matrix of scores (right hand side),

\( J \) = information matrix,

\( J^{-1} \) = inverse of information matrix
(variance–covariance matrix).

The expected means for different generations were then calculated
from the inverse matrix. The test of goodness of fit was done by
calculating chi-square (\( \chi^2 \)) using following formulae.

\[ \chi^2_{(n-p)} = \sum_{i}^{n} (O_i - E_i)^2 Wi \]

Where,

\( O_i \) = observed mean of \( i^{th} \) generations,

\( E_i \) = expected mean of \( i^{th} \) generations,

\( Wi \) = weight of \( i^{th} \) generation,

\( n \) = number of generation means available,

\( p \) = number of parameter estimated.
The standard error of each parameter (Pi) was calculated as,

\[ SE (P_i) = \sqrt{C_{ii}} \]

Where,

\( C_{ii} \) is the \( i^{th} \) diagonal elements of inverse matrix, \( J^{-1} \)

Models Fitted

Based on test of goodness of fit, when the simple additive dominance model failed to explain variation among generation means, a six parameter model proposed by Jinks and Jones (1985) was applied using following formula.

\[
\begin{align*}
  m &= 0.5\bar{P}_1 + 0.5\bar{P}_2 + 4F_2 - 2BC_1 - 2BC_2 \\
  (d) &= 0.5\bar{P}_1 - 0.5\bar{P}_2 \\
  (h) &= 6BC_1 + 6BC_2 - 8\bar{F}_2 - \bar{F}_1 - 1.5\bar{P}_1 - 1.5\bar{P}_2 \\
  (i) &= 2BC_1 + 2BC_2 - 4F_2 \\
  (j) &= 2BC_1 - \bar{P}_1 - BC_2 + \bar{P}_2 \\
  (l) &= \bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 + 4\bar{F}_2 - 4BC_1 - 4BC_2
\end{align*}
\]
The variances and standard errors of each estimate were computed as follow

\[
V_m = 0.25V_{p_1} + 0.25V_{p_2} + 16V_{F_2} + 4V_{BC_1} + 4V_{BC_2}
\]

\[
V(d) = 0.25V_{p_1} + 0.25V_{p_2}
\]

\[
V(h) = 36V_{BC_1} + 36V_{BC_2} + 64V_{F_2} + V_{p_1} + 2.25V_{p_1} + 2.25V_{p_2}
\]

\[
V(i) = 4V_{BC_1} + 4V_{BC_2} + 16V_{F_2}
\]

\[
V(j) = 4V_{BC_1} + V_{p_1} + 4V_{BC_2} + V_{p_2}
\]

\[
V(l) = V_{p_1} + V_{p_2} + 4V_{F_2} + 16V_{F_2} + 16V_{BC_1} + 16V_{BC_2}
\]

\[
SE(m) = \sqrt{V_m} \quad SE(i) = \sqrt{V_i}
\]

\[
SE(d) = \sqrt{V_d} \quad SE(j) = \sqrt{V_j}
\]

\[
SE(h) = \sqrt{V_h} \quad SE(l) = \sqrt{V_l}
\]

The test of significance of each parameter was done by usual t-test.

When any one of the parameters of digenic interaction found non-significant, the analysis was done as per best possible estimates by omitting that parameter according to Cavalli’s (1952) least square method.
3.7.3 Heterosis and inbreeding depression

The heterotic effects in term of superiority of F\textsubscript{1} over mid parent value (relative heterosis) according to Briggle (1963) and over better parent (heterobeltiosis) as per Fonseca and Patterson (1968) were worked out as under

\[
\text{Heterosis over mid parent (MP)} = \frac{F_1 - MP}{MP} \times 100
\]

\[
\text{Heterosis over better parent (BP)} = \frac{F_1 - BP}{BP} \times 100
\]

The inbreeding depression (ID) in F\textsubscript{2} generation was calculated as,

\[
\text{Inbreeding depression (\%)} = \frac{F_1 - F_2}{F_1} \times 100
\]

Where,

- $F_1$ = mean of F\textsubscript{1} generation
- $BP$ = mean of better parent
- $MP$ = mid parent value i.e. $(\bar{F}_1 + \bar{F}_2)/2$
- $F_2$ = mean of F\textsubscript{2} generation

The standard errors for heterosis and inbreeding depression were calculated as,
SE for (BP) \[= \sqrt{V_{F_1} + V_{BP}}\]

SE for (MP) \[= \sqrt{V_{F_1} + (V_{F_1} + V_{F_2})/2}\]

SE for inbreeding depression \[= \sqrt{V_{F_1} + V_{F_2}}\]

The test of significance for heterosis and inbreeding depression was done by usual t-test.

### 3.7.4 Number of genes controlling character

The following formulae proposed by Wright (1968) were used to estimate the number of genes segregating for the characters studied. These formulae are based on the assumptions that the segregating genes are in one parent only, not linked, have equal effects, have equal degree of dominance, act in same direction and that interaction components (i), (j), (l) are not important.

<table>
<thead>
<tr>
<th>Population tested</th>
<th>Formulae used</th>
</tr>
</thead>
<tbody>
<tr>
<td>Backcross to the rich parent</td>
<td>[n_1 = \frac{(GR_1)^2}{4[V_{BC_2} - (V_{p_2} + V_{F_1})/2]}]</td>
</tr>
<tr>
<td>F_2 generation</td>
<td>[n_2 = \frac{(GR_2)^2[1.5 - 2h(1 - h)]}{8[V_{F_2} - (V_{p_1} + V_{p_2} + 2V_{F_1})/4]}]</td>
</tr>
</tbody>
</table>
Where,

\[ h = \frac{(F_1 - P_2)}{(P_1 - P_2)} \]

\( GR_1 \) = genotypic range, estimated as the phenotypic range of the segregating generation (F\(_2\))

\( GR_2 \) = the difference between the two parents

\( \bar{P}_1 \) = the mean of the poor parent for respective character

\( \bar{P}_2 \) = the mean of the rich parent for respective character

\( V_{P_1} \) = the variance of the poor parent for respective character

\( V_{P_2} \) = the variance of the rich parent for respective character

\( V_{F_1} \) = the variance of the F\(_1\) generation

\( V_{F_2} \) = the variance of the F\(_2\) generation

\( V_{bc_2} \) = the variance of the rich parent for respective character’s backcross generation
3.7.5 Heritability and genetic advance

Heritability in narrow sense

Heritability in narrow sense was estimated as per method of Warner (1952)

\[ h^2 = \frac{2V_{F_2} - \left[V_{BC_1} + V_{BC_2}\right]}{V_{F_2}} \]

Where,

- \( h^2 \) = heritability in narrow sense,
- \( V_{F_2} \) = variance of mean of the \( F_2 \) generation
- \( V_{BC_1} \) = variance of mean of the backcross one generation,
- \( V_{BC_2} \) = variance of mean of the backcross two generation.

Genetic advance (GA)

Expected genetic advance (GA) was calculated according to the formula given by Johnson et al. (1955).

\[ G_S = k \cdot h^2 \cdot \frac{\sqrt{V_{F_2}}}{\sqrt{V_{F_2}}} \]

and

\[ \text{GA as (\% of mean)} = \frac{G_S}{X} \times 100 \]
Where,

\[ k = \text{selection coefficient at 5\%} \]

\[ \text{selection intensity equal to 2.06} \]

\[ h^2 = \text{heritability narrow sense}, \]

\[ \bar{X} = \text{mean of F}_2 \text{ population}, \]

\[ V_{F_2} = \text{variance of F}_2 \text{ generation} \]

### 3.7.6 Genetic correlations between traits.

Phenotypic covariance of a pair of traits was estimated in F\textsubscript{2} generation. The mean phenotypic covariance calculated for F\textsubscript{1} generation was considered as an estimate of the environmental covariance. Genetic correlations (r\textsubscript{G}) were estimated as per Falconer and Mackay (1996).

\[ r_{GXY} = \frac{\text{Cov}_{F_2}(xy) - \text{Cov}_{F_1}(xy)}{\sqrt{(V_{F_2}x - V_{F_2}x)(V_{F_2}y - V_{F_2}y)}} \]
Where,

\[ r_G (XY) = \text{genetic correlation between X and Y characters in F}_2 \text{ generation} \]

\[ \text{Cov } F_2 (XY) = \text{observed covariance of F}_2 \text{ generation between X and Y characters} \]

\[ \text{Cov } F_1 (XY) = \text{observed covariance of F}_1 \text{ generation between X and Y characters} \]

\[ V_{F2} X = \text{observed variance of F}_2 \text{ generation for X characters} \]

\[ V_{F1} X = \text{observed variance of F}_1 \text{ generation for X characters} \]

\[ V_{F2} Y = \text{observed variance of F}_2 \text{ generation for Y characters} \]

\[ V_{F1} Y = \text{observed variance of F}_1 \text{ generation for Y characters} \]

\[ S.E(r_G) = \frac{1 - r_G^2}{\sqrt{N - 2}} \]

Where,

\[ \text{SE } r_G = \text{standard error of genetic correlation between X and Y characters in F}_2 \text{ generation.} \]

\[ N = \text{number of plants observed in F}_2 \text{ generation} \]

The test of significance of \( r_G \) was done by usual t-test with n-2 degree of freedom.

\[ t = \frac{r_G}{SE(r_G)} \]
IV. RESULTS AND DISCUSSIONS

The estimates of heterosis and inbreeding depression together provide information about the type of gene action involved in the expression of various quantitative traits. Generation mean analysis is a simple and useful technique for characterising gene effects for the knowledge on the nature and magnitude of gene effects operative in the yield and yield related components would be useful for the development of better cultivars (Dhillon et al., 2000). The greatest benefit of this technique lies in the feasibility of the estimate of epistatic gene effects viz., additive x additive (i), additive x dominance (j) and dominance x dominance (l) in addition to additive (d) and dominance (h) effects. The effectiveness with which the selection of genotypes can be based on phenotypic performance is indicated by the heritability. But heritability itself provides no indication of the amount of genetic gain. The heritability along with the knowledge of genetic advance is more useful for predicting the gain of selection (Johnson et al., 1955). The correlation study gives an idea of amount of relationship between any pair of characters. The study of such associations among the characters is of immense importance to get information regarding exercising selection pressure in relation to yield attributes for genetic improvement.

In the present study, genetic analysis for slow leaf-rusting and eight yield related traits using six generations, namely $P_1$, $P_2$, $F_1$, $F_2$, $BC_1$ and
BC$_2$ of four bread wheat crosses, *viz.*, Lok 1 x HD 2189 (Cross 1), J 24 x HD 2189 (Cross 2), J 24 x HS 347 (Cross 3) and Kalyan Sona x HS 347 (Cross 4), hereafter referred to as Cross 1, Cross 2, Cross 3 and Cross 4 respectively, was carried out. The results obtained in this study are presented and discussed in following paragraphs.

### 4.1 Genetics for slow leaf-rusting

Leaf rust was first observed in 56 days old plants of J 24 and Kalyan Sona cultivars. Leaf rust intensity was increased as the plant approaches to wards maturity and it was found that per cent leaf rust intensity was observed at maturity stage in J 24 and Kalyan Sona parents. While in case of Lok 1 comparatively lower intensity of leaf rust was noticed from beginning to maturity with zero and 60 per cent disease intensity, respectively. On the other hand, the genotypes *viz.*, HD 2189 and HS 347 were observed to be slow leaf-rusting. In both the genotypes, leaf rust was observed at 70 days old plants and the progress of disease development was very slow up to maturity with only 3 and 10 per cent disease intensity was observed at maturity stage in HD 2189 and HS 347, respectively (Fig.1).

#### 4.1.1 Analysis of variance

The analysis of variance for experimental design for per cent leaf rust infection measured in term of area under disease progress curve (AUDPC) in four bread wheat crosses presented in Table 4.1 revealed
that mean squares due to crosses (between families) were significant for per cent leaf rust infection (AUDPC). The analysis of variance between progenies within families indicated that the differences among the generation means were significant for this in all the crosses. The Bartlet’s test for homogeneity of variances applied to the error mean squares revealed that error variances were significant for this trait indicating heterogeneity of error variances.

4.1.2 Mean performance

The mean values of parents, F₁, F₂ and backcross generations for per cent leaf rust infection measured as area under disease progress curve (AUDPC) in four bread wheat crosses presented in Table 4.2 indicated that variations among the generations found significant in all the crosses. Parents of Cross 1 differed significantly from each other as Lok 1 was susceptible parent and HD 2189 was resistant parent for slow leaf-rusting. The F₁ mean was intermediate between two parents indicating partial dominance for this trait. The F₁ and F₂ means while being at par with each other differed significantly from both the parents due to differences in genetic makeup of the parents involved. The BC₁ and BC₂ means were at par with their backcross parent Lok 1 and HD 2189, respectively.

The parents of Cross 2 differed significantly from each other as J 24 and HD 2189 was susceptible and resistance parents respectively for slow leaf-rusting. The mean value of F₁ generation while being in
Fig. 4. Area under disease progress curve (AUDPC) in parents used in the study.
between the parental means differed significantly from either of the parents, revealing partial dominance for AUDPC. The parity of mean value of the $F_1$ and $F_2$ generations suggested the involvement of additive gene action in the expression of this trait. The $BC_1$ and $BC_2$ means in between the parented limits but toward the direction of its respective recurrent parents $J\ 24$ and $HD\ 2189$, respectively. However, mean of $BC_1$ and $BC_2$ differed significantly from both the parents.

The Cross 3 revealed significant differences between the parents because $J\ 24$ was susceptible parents while HS 347 was resistance parent in the cross. The mean values of $F_1$ and $F_2$ generations were at par with each other and differed significantly from both the parents, indicating influence of additive gene action for this character. The mean value of $BC_1$ generation exceeded its recurrent parent $J\ 24$. The mean value of $BC_2$ generation was toward its backcross parent HS 347 but the difference between them was found significant.

The mean values of parents in the Cross 4 differed significantly as Kalyan Sona was susceptible parent and HS 347 was resistant parent in this cross. The mean values of $F_1$, $F_2$, $BC_1$ and $BC_2$ were in between the parental limits were at par with the parent HS 347, suggesting dominance gene action for slow leaf-rusting.
4.1.3 Heterosis and inbreeding depression

The results of present study on heterosis over mid parent, heterosis over better parent and inbreeding depression in F$_2$ generation for AUDPC in four bread wheat crosses are presented in Table 4.3. Low value of percent AUDPC is desirable and parent with slow rust expression was taken as better parent for calculating heterosis over better parent. The estimate of the heterosis over mid parent in all the crosses was significant and negative with the range of –3.94 % (Cross 3) to –53.63 % (Cross 4). All the four crosses expressed highly significant positive heterosis over better parent and the range was observed from 9.40 % (Cross 4) to 286.81 % (Cross 2), which indicated that F$_1$ plants in all the crosses were more susceptible to leaf rust than their respective resistant parents and genes for slow-rusting were observed to be partial dominance in nature. The wider range of heterosis over better parent indicated that more number of alleles is fixed on resistant parent and lesser of number alleles on susceptible parent (Bjarko and Line, 1986b). The positive heterosis over better parent and negative heterosis over mid parent expressed by same cross combination indicated that partial dominance of slow-rusting genes was responsible for this character in the crosses studied.

A perusal of the date on inbreeding depression for AUDPC (Table 4.3) indicated that the value of inbreeding depression varied from –11.08 % (Cross 3) to 43.51 % (Cross 4). All the four crosses showed
significant and negative inbreeding depression in F$_2$ for this trait. Significant and positive heterosis over better parent along with significant and negative inbreeding depression indicated complex nature of gene action for slow-rusting.

4.1.4 Gene effects

The basic set of six generation means for each of the four crosses were used to estimate various gene effects for slow leaf-rusting in bread wheat. Scaling tests A, B and C of Mather (1949) and joint scaling tests proposed by Cavalli (1952) were employed to detect the presence of epistasis. The characters showing digenic interactions were subjected to six parameter model advocated by Jinks and Jones (1958). In order to achieve the precision of the estimated parameters, best fitted model was run after omitting non-significant interaction.

The results presented in Table 4.4 for per cent leaf rust infection measured as area under disease progress curve (AUDPC) revealed that the scaling test A was significant for all the crosses except Cross 2 while, scaling B was significant for Cross 2 and 4. The scaling C was significant for all the crosses except Cross 4. The results presented in Table 4.4 revealed that out of three scales, i.e. A, B and C any two scales were significant in all the crosses. This suggested the presence of non-allelic interaction for slow-rusting in all the crosses.
The analysis of gene effects indicated that the main effects, additive (d) and dominance (h) were significant for all the crosses, except (h) in the Cross 2 and 4. The additive gene effects (d) showed positive sign for all the crosses, while the direction of dominance (h) effects being negative in all the crosses except Cross 1. The relative magnitude of (h) was higher than the additive (d) effect in Cross 1 and 3 which, indicated the preponderance of dominance (h) effect over the additive (d) effect for this trait in Cross 1 and 3.

Among the digenic effects, additive x additive (i) effects was significant and positive in Cross 3. While additive x dominance (j) effects and dominance x dominance (l) effects were found significant in all the crosses. Among four crosses, Cross 1 and 3 had positive sign for (j) effect, whereas Cross 2 and 4 had negative sign. Incase of (l) effects all the crosses found negative sign.

The relative magnitude of additive gene effects was higher in Cross 2 and 4 with complementary epistasis effects, indicating simple selection would be effective for improvement for slow leaf-rusting. Skovmand et al. (1978), Singh et al. (1986), Geeta Tondon et al. (1989), Jacobs and Brores (1989) and Das et al. (1992) observed preponderance of additive gene effect for slow-rusting in wheat. Therefore, present findings corroborated the results reported by these early workers.
On other hand, in Cross 1 and 3, non-additive effects were higher than additive gene effect, indicating importance of nonfixable gene effects in the expression of the trait. However, the sign of \((h)\) and \((l)\) being opposite, indicating involvement of duplicate epistasis in Cross 1. In such cases, difficulties in the improvement for slow leaf-rusting through selection. However, exploitation of transgressive segregation in some of these crosses to select for leaf rust resistant plants from segregating generation could be possible. Saini (1979), Khurana (1981), Chawla et al. (1990), Kaul et al. (1991), Pawar et al. (1992), Yadav et al. (1992) and Dalal and Singh (1994), reported additive as well as non-additive gene effects for this trait with preponderance of non-additive effect for governing slow-rusting in wheat. Present findings were in agreement with the results reported by these early workers.

4.1.5 Variability and number of gene groups

The study of variability is pre-requisite for any crop improvement programme. The estimates of heritability in narrow sense, along with genetic advance as per cent of mean are most useful than the heritability value alone in predicting the effect of selection. The results obtained for per cent leaf rust infection on variability and number of gene groups in four bread wheat crosses are presented and discussed here under.

Three crosses \(v\text{\"i\text{\"c}}\), Cross 1, 3 and 4 had transgressive segregation in \(F_2\) for desirable direction, while in the four bread wheat crosses all the
four crosses exhibited transgressive segregation in F2 for undesirable direction (Table 4.5). Therefore, selection of leaf rust resistant plant and high yielding ability from F2 generation in Cross 1, 3 and 4 could be possible for improvement of a particular lines.

The estimates of heritability ranged from 42.63 % (Cross 2) to 78.27 % (Cross 3). The magnitude of heritability was high in the Cross 1, 3 and 4 and moderate in the Cross 2. High narrow sense heritability for AUDPC as recorded in the Cross 1, 3 and 4 indicated that the variations among the genotypes were mostly genetic, but in case of the Cross 2 environment might have played a major role to cause such variations. On the other hand, values of genetic advance as percentage of mean for slow-rusting character AUDPC varied from 45.14 % (Cross 2) to 88.07 % (Cross 1). This indicated that the magnitude of genetic advance was high in all the crosses, high magnitude of heritability and genetic advance in the Cross 1, 3 and 4 indicated that AUDPC in these crosses was under the control of additive gene actions and simple selection method could be effective for developing slow-rusting genotypes.

Since the extent of improvement of character would depend not only on heritability but also on the extent of phenotypic variation in the population in which the selection is to be made, the heritability in relation to genetic advance should be viewed for predicting the effectiveness of selection. The moderate heritability along with high genetic advance as
observe in the Cross 3 indicated that high genetic advance was always not associated with high heritability. Inconsistence in the magnitude or heritability and genetic advance for this trait may be attributed to high phenotypic standard deviation. High phenotypic deviation may tend to high genetic advance. Thus, the variability in base population would be more useful than the magnitude of heritability alone for selecting better genotypes (Johnson et al. 1955). High heritability was reported for slow-rusting characters like AUDPC (Das et al., 1972) and latent period (Shaner et al., 1997).

The estimates of number of genes controlling the difference in percent leaf rust infection (AUDPC) calculated by two methods ranged from 0.06 to 12.47. The difference in the estimates by two methods was found to be larger. The first method (n₁) used the phenotypic range of the segregating population (backcross) as an estimate of the genotypic range. Because of environmental effects on the phenotypic range, especially in the F₂ and backcross population, this method over estimate actual number of gene pairs conditioning the differences for a given character. The second method (n₂) used the difference in parental means to estimate the genotypic range. Both the methods are based on the assumption that there are no linkages, no dominance and no epistasis existed for a given character. The presence of linkage, dominance and epistasis may cause
either an over estimation or an under estimation of the actual number of segregating genes.

The gene pair controlling slow-rusting was 1 to 13 in the material studied. The Cross 1 and 2 had common resistant parent HD 2189 and Cross 3 and 4 had common resistant parent HS 347. HD 2189 might have possessed 1 to 13 genes, while HS 347 might have possessed 1 to 3 genes for the differences in slow leaf-rusting. Different workers reported different number of genes responsible for conditioning leaf rust resistance in their material under study. Ohm and Shaner (1976) reported 2-12 genes, while Bjarko and Line (1986b) estimated 2 to 3 or even more gene groups conditioning leaf rust resistance. Jacobs and Broers (1989) reported that 0.1 to 19.6 effective factors were responsible for leaf rust resistance whereas Zhang et al. (2001) observed that 4 to 5 gene groups were found to be segregated for stripe rust resistance in bread wheat.

4.1.6 Correlations of per cent leaf rust infection (AUDPC) with grain yield and filling period related traits

The degree and manner of association between traits can be understood by studying their correlation coefficient. This measure gives an indication of association that may more useful to carry out reliable selection for yield improvement. The heritable association between two variables is known as genetic correlation. This type of correlation may either due to pleiotrophic action of genes or due to linkage or more likely
both (Falconer, 1960). This desirable type of correlation is more stable and is of paramount importance for a plant breeder to bring about genetic improvement in one character by selecting the other character of a pair. The relationship of yields contributing characters with per cent leaf rust infection (AUDPC) will aid to ensure effective selection for yield improvement with high degree or leaf rust resistance. The association between per cent leaf rust infection (AUDPC) and some yield related traits was studied in present investigation and results are presented and discussed as under.

The correlations between AUDPC and yield related traits presented in Table 4.6 revealed that correlations in four bread wheat crosses studied were inconsistent in all the pairs of character combinations. The association of per cent leaf rust infection was significant and positive with days to ear emergence in Cross 2 \(r = 0.311^{**}\) and in Cross 4 \(r = 0.26^{**}\) as well as significant and negative correlation with days to maturity in Cross 2 \(r = -0.314^{**}\) due to different genetical makeup of the parents for respective crosses. The association of per cent leaf rust infection was significant and positive with days to ear emergence and significant and negative correlation with days to maturity, which suggested that highly rust infected plants were late in ear emergence and early matured. Similar findings of significant and positive correlation of per cent leaf rust infection with days to anthesis were reported by Ohm
and Shaner (1976). While, Skovmad et al., (1978) and Veena Chawla et al. (1990), reported significant and negative correlation of per cent leaf rust infection and days to maturity in bread wheat. Thus, present findings are akin to the results reported by these workers.

The association of per cent of leaf rust infection with vegetative period was significant and positive and two crosses i.e. Cross 2 (r = 0.304**) and 4 (r = 0.178*) which revealed that highly leaf rust infected plants were associated with longer vegetative period and vice a versa. Inconsistent results for this pair of characters was observed due to non-significant association in two crosses i.e. Cross 1 and Cross 3.

The association of per cent leaf rust infection with grain filling period (Table 4.6) was all the crosses showed non-significant values as this pair of character expressed non-significant association in all the four crosses. If we assume that the vegetative period plus grain filling period make up the days to maturity, they are expected to be correlated with it, but in the present study such relationship were not observed. The probable reasons for such differences in correlation may be the effect of high per cent leaf rust infection intensity stress in late season, which restricted the length of the growing period. Thus, if the genotype had a long vegetative period, it has forced to fill its kernels in the short period, where if it had a short vegetative period, then longer period was available for grain filling (Knott and Gebeyehou, 1987).
Correlation between the per cent leaf rust infection and number of leaves per plant were found negative and significant in Cross 3 ($r = -0.650^{**}$) indicating that if the per cent leaf rust intensity increase the number of leaves per plant decrease. To improve the population, selection could be done the more number of leaves per plant, which are leaf rust free in segregating plants. Correlation values between AUDPC and number of leaves per plant for remaining crosses were not worked out as these crosses failed to show significant differences among the generation means.

Out of four crosses studied, per cent leaf rust infection (AUDPC) was correlated significantly and positively with plant height (Table 4.6) only in the Cross 3 ($r = 0.276^{**}$). Das et al. (1992) reported that leaf rust and plant height had weaker correlation, which are akin to the results reported by the worker. The relationship between these characters was non-significant in the Cross 1 and 4, while Cross 2 was dropped from the analysis due to non-significant differences among the generation means.

In Cross 2 significant and positive correlation ($r = 0.218^{**}$) was observed between per cent leaf rust infection (AUDPC) and 100-grain weight (Table 4.6). While in Cross 4 significant and negative correlation ($r = -0.166^*$) was found for this pair of trait. The positive correlation in Cross 2 and negative correlation in Cross 4 was observed due to variable difference in the parents of transgressive segregation in $F_2$ of both the
crosses. Correlation coefficient were non-significant between per cent leaf rust infection (AUDPC) and 100-grain weight in Cross 1 and 3. This indicated that independent nature of per cent leaf rust infection (AUDPC) and 100-grain weight.

Out of four crosses, two crosses i.e. Cross 1 and 3 exhibited significant and negative correlations between per cent leaf rust infection and grain yield per plant. Such negative relationship between grain yield per plant and per cent leaf rust infection would be possible as infection of this disease causes reduction in quantity of assimilates to be available for grain development and ultimately reduces the grain yield (Cox et al., 1997). Grain yield per plant was found to be independent of per cent leaf rust infection in the Cross 2 and 4 as evidenced by non-significant values.

Thus, the results of present study revealed that analysis of variance between families as well as analysis of variance between progenies within families were found significant in all the four bread with crosses. The parents of all the four bread wheat crosses differed significantly respective each other parent because F₁ involved one resistant parent and next susceptible parent. The mean values of F₁ and F₂ were intermediate between respective parents indicating partial dominance for this trait. The mean values of BC₁ and BC₂ differed significantly from each other for Cross 1 and 3 and in general where towards the respective recurrent
parent. The significant and negative heterosis over mid parent and inbreed depression were observed for all the four bread wheat crosses.

The presence of epistasis as determined by scaling test of Mather (1949) and joint scaling test of Cavalli (1952) was evident for all the bread wheat crosses. The estimates of additive (d) and dominance (h) components on best fitting model were significant for this trait in all the four bread wheat cross except (h) in Cross 2 and 4. Among the digenic interactions parameters additive x additive (i) effect in Cross 3, additive x dominance (j) effect in all the four bread wheat crosses and dominance x dominance (l) effect in Cross 1, 2 and 3 were found to be significant indicating involvement of both fixable and non-fixable gene effects in the expression of the trait.

The estimates of heritability ranged from 42.63 per cent (Cross 2) to 78.27 per cent (Cross 3) and genetic advance as per cent of mean from 45.14 per cent (Cross 2) to 88.07 per cent (Cross 1) which indicated that additive gene action played a major role in the inheritance of slow leaf-rusting in all the crosses except Cross 2.

Number of gene pair controlling slow leaf-rusting indicated that zero to twelve in Cross 1, 1 to 13 in Cross 2, 2 to 3 in Cross 3 and zero to three in Cross 4 conditioning the slow leaf-rusting in each parent using $n_1$ and $n_2$ procedure of Write (1968), respectively.
The significant and positive correlation coefficient of per cent leaf rusting with days to ear emergence vegetative period and 100-grain weight was observed in Cross 2 and 4 except with 100-grain weight in Cross 4. Similarly significant and positive association of per cent leaf rust infection with plant height was found in Cross 3 only. On the other hand, significant and negative correlation coefficient of per cent leaf rust infection with days to maturity and 100-grain weight in Cross 4 as well as with grain yield in Cross 1 and 3 and plant height in Cross 3 was recorded.
REFERENCES


* Original not seen
### Appendix-I Mean Weekly Weather Data during 2004-05 recorded at Instructional Farm, Junagadh Agricultural University, Junagadh.

<table>
<thead>
<tr>
<th>Std. Week No.</th>
<th>Temp. C°</th>
<th>R.H.%</th>
<th>W.S. (kmph)</th>
<th>BSS (hrs)</th>
<th>Evapo. (mm)</th>
<th>Rain (mm)</th>
<th>Rainy Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>40</td>
<td>32.9</td>
<td>24.1</td>
<td>84</td>
<td>63</td>
<td>5.6</td>
<td>7.4</td>
<td>3.7</td>
</tr>
<tr>
<td>41</td>
<td>33.3</td>
<td>21.5</td>
<td>78</td>
<td>38</td>
<td>3.7</td>
<td>7.8</td>
<td>4.4</td>
</tr>
<tr>
<td>42</td>
<td>35.1</td>
<td>18.7</td>
<td>69</td>
<td>27</td>
<td>2.1</td>
<td>8.6</td>
<td>4.3</td>
</tr>
<tr>
<td>43</td>
<td>36.3</td>
<td>18.0</td>
<td>62</td>
<td>21</td>
<td>2.0</td>
<td>9.3</td>
<td>4.5</td>
</tr>
<tr>
<td>44</td>
<td>35.5</td>
<td>20.8</td>
<td>59</td>
<td>26</td>
<td>2.5</td>
<td>6.5</td>
<td>4.7</td>
</tr>
<tr>
<td>45</td>
<td>35.3</td>
<td>19.9</td>
<td>55</td>
<td>23</td>
<td>2.9</td>
<td>7.1</td>
<td>5.3</td>
</tr>
<tr>
<td>46</td>
<td>36.1</td>
<td>21.3</td>
<td>69</td>
<td>32</td>
<td>2.2</td>
<td>7.3</td>
<td>4.1</td>
</tr>
<tr>
<td>47</td>
<td>35.5</td>
<td>17.8</td>
<td>70</td>
<td>22</td>
<td>2.4</td>
<td>8.5</td>
<td>4.3</td>
</tr>
<tr>
<td>48</td>
<td>34.1</td>
<td>15.8</td>
<td>66</td>
<td>23</td>
<td>2.2</td>
<td>8.6</td>
<td>4.0</td>
</tr>
<tr>
<td>49</td>
<td>33.2</td>
<td>15.8</td>
<td>66</td>
<td>25</td>
<td>2.7</td>
<td>7.7</td>
<td>4.1</td>
</tr>
<tr>
<td>50</td>
<td>34.5</td>
<td>14.3</td>
<td>62</td>
<td>19</td>
<td>2.7</td>
<td>8.3</td>
<td>4.5</td>
</tr>
<tr>
<td>51</td>
<td>31.8</td>
<td>14.5</td>
<td>76</td>
<td>34</td>
<td>3.0</td>
<td>5.7</td>
<td>3.2</td>
</tr>
<tr>
<td>52</td>
<td>29.9</td>
<td>15.0</td>
<td>71</td>
<td>36</td>
<td>3.1</td>
<td>4.5</td>
<td>3.5</td>
</tr>
<tr>
<td>1</td>
<td>24.7</td>
<td>11.3</td>
<td>90</td>
<td>40</td>
<td>6.6</td>
<td>0.2</td>
<td>4.9</td>
</tr>
<tr>
<td>2</td>
<td>27.3</td>
<td>11.0</td>
<td>76</td>
<td>31</td>
<td>4.0</td>
<td>7.2</td>
<td>3.6</td>
</tr>
<tr>
<td>3</td>
<td>25.7</td>
<td>13.3</td>
<td>42</td>
<td>15</td>
<td>6.0</td>
<td>9.1</td>
<td>5.1</td>
</tr>
<tr>
<td>4</td>
<td>27.5</td>
<td>12.2</td>
<td>46</td>
<td>27</td>
<td>10.6</td>
<td>9.0</td>
<td>7.0</td>
</tr>
<tr>
<td>5</td>
<td>30.9</td>
<td>12.0</td>
<td>66</td>
<td>25</td>
<td>6.9</td>
<td>8.4</td>
<td>5.3</td>
</tr>
<tr>
<td>6</td>
<td>29.2</td>
<td>08.8</td>
<td>71</td>
<td>22</td>
<td>6.0</td>
<td>8.1</td>
<td>6.1</td>
</tr>
<tr>
<td>7</td>
<td>28.0</td>
<td>10.5</td>
<td>64</td>
<td>26</td>
<td>6.8</td>
<td>8.5</td>
<td>6.0</td>
</tr>
<tr>
<td>8</td>
<td>28.5</td>
<td>09.4</td>
<td>63</td>
<td>21</td>
<td>7.0</td>
<td>7.0</td>
<td>5.9</td>
</tr>
<tr>
<td>9</td>
<td>30.7</td>
<td>09.3</td>
<td>73</td>
<td>37</td>
<td>8.9</td>
<td>8.8</td>
<td>4.0</td>
</tr>
<tr>
<td>10</td>
<td>29.6</td>
<td>14.0</td>
<td>75</td>
<td>39</td>
<td>5.1</td>
<td>8.5</td>
<td>3.7</td>
</tr>
<tr>
<td>11</td>
<td>28.0</td>
<td>12.0</td>
<td>86</td>
<td>35</td>
<td>5.6</td>
<td>5.2</td>
<td>4.1</td>
</tr>
<tr>
<td>12</td>
<td>28.8</td>
<td>11.7</td>
<td>86</td>
<td>24</td>
<td>2.5</td>
<td>5.8</td>
<td>3.2</td>
</tr>
<tr>
<td>13</td>
<td>28.8</td>
<td>09.7</td>
<td>73</td>
<td>24</td>
<td>2.8</td>
<td>5.4</td>
<td>3.8</td>
</tr>
</tbody>
</table>