Review of Literature
2. REVIEW OF LITERATURE

2.1. Heterosis and Combining ability studies

In the utilization of hybrid vigour in commercial crops only that vigour in excess of the better parent is useful for plant breeders. Heterosis often described as increase in the vigour and fertility of the hybrid over the mid-parent or the better parent. An excellent review on heterosis in wheat was done in the past by Briggle (1963).

To exploit heterosis on a commercial scale, it is necessary to identify parents which show strong heterotic effects. Several studies in the 1960s such as Briggle et al. (1964), Bhatnagar and Sharma (1967), Jain and Anand (1969) have indicated the presence of a high degree of heterosis in bread wheat. Walton et al. (1971), Khotyleva et al. (1973), Halloran, (1975) and Malik et al. (1981) reported heterosis for yield and various yield components in wheat. Pronounced heterotic effects were reported among related varieties of spring wheat varieties. (McNeal et al.,1965), and among winter wheat varieties (Brown et al., 1966; Kronstad et al., 1964; Patterson et al., 1966; Santiago Fonseca et al.,1968). In India, Karamchand and Randhawa (1981) reported heterosis over the better parent ranging from 44 to 52 percent for grain yield where as Patwary et al. (1986) found positive heterosis for all the agronomical characters studied, except days to flowering. F₁ hybrids yielding upto 75 - 84% more than the higher yielding parent have been reported in several cross combinations of wheat (Fonseca and Patterson, 1964). Dhindsa et al. (1977) and Sharma et al. (1989) observed heterosis for grain weight, grain yield and other yield components in a group of Indian and Mexican cultivars. Several other studies have also demonstrated significant heterosis for various qualitative and quantitative characters in bread wheat (Deshpande and Nayeem, 1999; Shekhawat et al., 2000). Kaltsikes and Lee (1971), Widner and Lebsock (1973) and Dhonukshe et al. (1979) reported heterosis for days to maturity, plant height, tiller number, kernel number per spike and kernel weight in durum and bread wheat. In a set of diallel crosses in wheat,
substantial heterosis over the better parent for grain yield was reported by Atale and Vitkare (1990). Similar outcomes were obtained for various other agronomic characters in wheat and related cereals (Yadav and Murty, 1976; Jatasra et al., 1980). Egorkina et al. (1990), Thakur et al. (1991), Chaudhary et al. (1993), Salgotra et al. (2002) and Joshi et al. (2004) estimated heterosis in intervarietal crosses of either spring or winter wheats.

Mahajan et al. (1999) proposed the commercial exploitation of heterosis through the production of hybrid wheat making use of a chemical hybridizing agent. Their study involved in an attempt to evaluate a chemical hybridizing agent and to use it to produce hybrids, and, to identify parental lines that exhibit commercial by exploitable heterosis.

Combining ability estimates provide a useful tool to select parents with maximum potential for transmitting desirable gene combinations to their progeny. Griffing (1956) was the first to measure the combining ability. The utility of the Line x Tester design (Kempthorne, 1957) to determine the relative capacity of a number of female and male parents to produce desirable hybrids is well-known. Detailed studies using this design were done by Murty et al. (1967) in Pennisetum typhoids, Rao et al. (1968) in sorghum, and Gill et al. (1974) in bread wheat. In triticale, Singh and Chowdhury (1977) reported that the best hybrids usually result from either the best performing variety or from the best general combiner. Jag Shoran et al. (1984) studied the F₂ generation from a Line x Tester crosse; to obtain general combining ability estimates. The estimates of general combining ability effects showed which parents involved were the best general combiners for grain yield and yield contributing characters. Shripal and Singh (1989) studied the F₁ from a Line x Tester analysis. They found that specific combining ability variances were significant for all characters except number of grains per ear and ear length. Number of spikelets per ear and biological yield also had significant general combining ability variance indicating the importance of both additive and non additive components. Aruna and Raghavaiah (1998), on the other hand, found that both GCA and SCA variances
were important for most of the yield components and also for protein content and pelshenke value, which can be improved using any breeding method (for instance, biparental mating) that can exploit both additive and non-additive gene systems. Maloo (1992) concluded that additive gene action was more important than non-additive as the GCA variances were higher compared to SCA variances. Sharma and Garg (2001) studied combining ability in four different normal and saline environments using a Line x Tester design for grain yield and its components. They noticed high GCA and SCA for grain yield. In rice, Radhidevi et al. (2002). Found that non-additive gene action was more important for most of the characters studied except for days to 50% flowering and panicle length, which provide scope for the exploitation of hybrid vigour through heterosis breeding. In durum wheat, Chovatia and Jadon (1989) did combining ability analysis studies over environments. Their results revealed that both GCA and SCA components of variance were significant for all the characters. Chauhan et al. (1976) studied combining ability effects in F2 and F3 generations in wheat. They found that GCA variances were predominant in both the generations. However, the GCA and SCA estimates were substantially lower than those of an F1 diallel. Similar results were reported by Borojevic (1963), Paroda and Joshi (1970a) and Smocek (1971) for yield and other characters both in the F1 and F2 generations. Jag Shoran et al. (1984) observed significant variation for general combining ability and specific combining ability for grain weight per main spike, grain number per main spike, 1000-grain weight and grain yield per plant suggesting that both additive and non-additive genetic components were important in determining the inheritance of these characters. Paroda and Joshi (1970b), Singh et al. (1974) and Jatasra and Paroda (1978) reported similar results for the same characters. Singh et al. (1985) observed that per se performance of the parent is closely related with the general combining ability effect. Most of the crosses with high specific combining ability effects had at least one good general combiner parent.
The Diallel cross technique has long been used to obtain information, about the breeding values of lines.

Diallel analysis in wheat has been reported by many workers, but information on diallel analyses of wheat done environments is scanty. Moreover, it is known that quantitative characters are influenced by the environment. Dasgupta and Mondal (1988) studied combining ability with respect to seed yield per plant in a half-diallel cross over two years. Their results indicated that both GCA and SCA variances were important for the characters. Iqbal Singh et al. (1991) did combining ability studies for harvest index, biological yield and grain yield in timely and late sowings. The GCA variance was significant only for harvest index, while the SCA variances were significant for all three characters. Iqbal Singh and Paroda (1987) and Iqbal Singh and Singh (1994) proposed the use of partial diallel analyses for calculation of combining abilities in normal and stress environments. The characters days to heading, plant height, grains per ear, 1000-grain weight and harvest index were mainly under the control of additive gene effects, while for the characters tiller number, biological yield and grain yield there was preponderance of non-additive gene effects. Gill et al. (1979) reported stronger general combining ability effects for spike length, plant height and peduncle length, whereas the specific combining ability components of variances were higher for grain yield and grain weight. Singh et al. (1982) found significant correlations between parental means and GCA values. Maloo (1987) reported that GCA variances were higher than SCA variances in both normal and late plantings for all the characters he studies. Mann and Sharma (1995) did combining ability analyses of $F_1$ and $F_2$ progenies and found significant differences for GCA among the parents and for SCA of among crosses for all the characters studied.

Talukdar and Bains (1983), Srivastava et al. (1992) and Sameena Sheikh and Iqbal Singh (2000) calculated combining ability effects for yield and morphological traits in different environments. Their results revealed GCA and SCA variances were significant for all the characters, and the environment has a
significant effect in the expression of almost all the traits. Singh et al. (2001) and Joshi et al. (2001) determined the relative proportions of additive and non-additive variances for yield, quality and disease reaction in F₁ and F₂ generations.

2.2. Breeding for rust resistance in hexaploid wheat

Resistance breeding is a vital component of disease management and its success depends on the availability of new sources of disease resistance. In polyploid genera, wild relatives of the cultivated species provide an important reservoir of genes for use in resistance breeding. The genus *Triticum* contains three ploidy levels and about 30 species (Dvorak and McGuire, 1991). Most of the species have been investigated as sources of disease resistance genes, and several of them have been successfully used to transfer disease resistance to *T. aestivum*. The amount of alien chromatin involved in these transfers varies from a single gene to a chromosome segment / arm or entire chromosome.


In the past successful attempts were made to transfer rust resistance genes from the wild wheats and other closely related species / genera to
cultivated wheat by backcrossing. Rust resistance genes from *T. monococcum* (The, 1973; Victor Vallega, 1992); *Ae. speltoides*, *Ae. umbellulata*, *Ae. comosa* and *Ae. squarrosa* (Rowland and Kerber, 1974; Kerber and Dyck, 1979, 1990; BenYehuda *et al.*, 2000; Menon and Tomar, 2001), *T. cylindrica* (Bai *et al.*, 1995); *T. araraticum* (Dyck, 1992); *Ae. triaristata* (Bai *et al.*, 1994); *T. miguschovae* (Davoyan and Ternovskaya, 1995); *T. turgidum* (Yahyaoui *et al.*, 2000); *T. timopheevii* (Johnson and Tanner, 1994); *Thinopyrum distichum* (Littlejohn *et al.*, 1992); *Th. bessarabicum* and *Th. curvifolium* (Almouslem *et al.*, 1998), *Th. ponticum* (Sawhney *et al.*, 1998); *Th. intermedium* (Tanget *et al.*, 2000); and other tetraploid wheats (Knott 1989a, Jiang *et al.*, 1994, Friebe *et al.*, 1996) were transferred to bread wheat by simple backcrossing. Disease resistance genes from rye and barley were also introduced in bread wheat (Acosta, 1962; Friebe *et al.*, 1990; Niks *et al.*, 1993). Introgressed genes derived from these programmes are freely accessible, and are being exploited throughout the world.

In India, Kochumadhavan *et al.* (1980) screened more than 200 indigenous and exotic hexaploid wheat stocks for leaf, stem and stripe rust resistance and a large number of them were shown to possess resistance to more than one type of rust. Field and seedling tests with selected single pathotypes recognized a minimum of six sources of adult plant resistance in Indian wheats (Sawhney *et al.*, 1991, 1992, 1998). Shiwi and Saini (1993) have postulated diverse adult plant leaf rust resistance genes in 28 Indian and 9 International cultivars, comprising 22 groups. Seedling tests also revealed a number of *Lr, Sr, Yr* genes in these wheat stocks (Nayar *et al.*, 1994, 1996; Nagarajan *et al.*, 1987). Some of the seedling and adult plant rust resistance genes were transferred to Indian wheat cultivars (Sawhney, 1994, 1995, 1997a, 1998a;b; Sawhney and Sharma, 1996, 1999; Brahma *et al.*, 1993; Asir *et al.*, 1994; Reddy *et al.*, 1995, 2001a; McIntosh *et al.*, 1996; Singh *et al.*, 1998; Mandeep Kaur, 2000; Tomar and Menon, 1998a,b; Patil *et al.*, 2000). Some of resistance genes, which are effective only in adult plants, were also transferred to commercial cultivars (Singh
In addition to providing rust resistance, a transferred rust resistance gene may also influence the yield of the recurrent wheat parent (Reddy and Aloka Saikia, 1994; Reddy and Viswanathan, 1999; Reddy, 2001; Reddy et al., 2001b). The yield will either be increased or decreased, depending upon whether the gene is closely linked to any undesirable genes. Griffey and Allan (1986) reported large reductions in grain yield when resistance genes for leaf rust and stripe rust were introduced in wheat. The et al. (1988) also noticed yield reduction of about 9% and 7% associated with stem rust resistance genes Sr26 and Sr21, respectively. Knott (1993) measured an average yield reduction of 11.5% when he analysed the influence of resistance genes for stem rust transferred to the cultivar Marquis. Ortelli et al. (1996a,b) recorded reduced yield in winter wheats carrying leaf rust resistance gene Lr9. On the other hand, wheats with 1B / 1R substitutions or translocations (carrying Sr31+Lr26+Yr9) are high yielders world wide (Payne et al., 1987; Rajaram et al., 1983,1988; Rogers et al., 1989; Lukaszewski, 1990; Sawhney and Sharma, 1999). Lobachev (1992) and Cox et al. (1997) observed that in addition to imparting high degree of rust resistance, leaf rust resistance genes Lr19 and Lr41 also increased the grain yield of the recurrent parent.

Once a targeted gene is incorporated into the recurrent parent, it is necessary to verify and confirm the transfers. If the resistance gene occurs on on alien chromosome segment that is sufficiently large e.g. an entire chromosome or chromosomal arm / segment, the alien material can be identified on the basis of cytogenetic studies (including C or N-banding). Using sequential chromosome banding and in situ hybridization, wheat lines carrying rust resistance genes Sr31+Lr26+Yr9, Sr24+Lr24, Sr25+Lr19 and Sr26 have been identified (Berzonsky and Francki, 1999; Jiang et al., 1994; Arumugam and Reddy, 1999a). If the introduced alien gene cannot be detected cytologically, other methods are used to confirm its presence. Singh (1987) and Dalmir Singh (1991) identified rye
gene(s) in wheat on the basis of morphological markers like hairy peduncle, brown spike and red grain. Sharma and Singh (1999, 2000) induced homoeologous recombination in the absence of chromosome 5B of wheat to transfer linked leaf and stem rust resistance genes from rye to selection 212. Presence of leaf rust resistance genes \( Lr10 \) and \( Lr14, Lr23 \) and \( Lr26 \) in two bread wheat cultivars, was confirmed by Nayar et al. (1988, 1991, 1993, 1996) and Mandeep Kaur et al. (2000) on the basis of rust infection types in \( F_2 \) seedlings derived from crosses between the resistant cultivar and a universally susceptible wheat variety, Agra Local. Kaushal and Upadhyaya (1995), Knott (2000) and Csosz et al. (2001) have detected the presence of stem rust resistance genes in several bread wheats on the basis of segregation in \( F_2 \) and \( F_3 \) populations derived from crosses between resistant near-isogenic lines and a susceptible parent. Inheritance, of rust resistance genes in monosomic and linkage analyses, also provided clues regarding the presence of newly transferred genes in wheat (Koebner and Shepherd, 1985; Mahmoud et al., 1987; Singh, 1991, 1992; McMillin et al., 1986, 1993; Bariana and McIntosh, 1992, 1993, 1994; Winzeler et al., 1995; Riede, et al., 1995a, b; Sridevi et al., 2000; Sharma and Singh, 2001; Dalmir Singh, 2002). Monosomic analyses aided in determining the chromosomal location of rust resistance genes like \( Lr41, Lr42 \) and \( Lr43 \) (Cox et al., 1994, 1997; Hussein et al., 1997), \( Lr45 \) (McIntosh et al., 1995a); stripe rust resistance genes \( Yr15 \) (McIntosh et al., 1996), \( Yr24 \) (McIntosh and Lagudah, 2000), \( Yr28 \) (Singh et al., 2000); powdery mildew resistance gene \( Pm22 \) (Peusha et al., 1996) and two undesignated complementary leaf rust resistance genes (Davoyan and Ternovskaya, 1996). Mena et al. (1989) used both biochemical and cytological markers to confirm transfer of \emph{Aegilops ventricosa} chromosomes to wheat. Various biochemical and cytological techniques were employed to detect the 1B / 1R translocation in wheat (Javornik et al., 1991; Friebe et al., 1992). The study of isozyme variation associated with added and substituted alien chromosomes and telosomes has been an effective method for identifying alien (Hart and Tuleen, 1983). Changes in biochemical compounds can often be used indirectly to confirm gene transfers.
(Reddy, 2000a). Such substances / enzymes, include storage proteins ((Payne et al., 1979, 1982, 1983; Burnouf and Bouriquet, 1980; Bullrich et al., 1998; Gupta and Shepherd, 1990; Gupta and Shepherd, 1992), peroxidase and polyphenol oxidase (Johnson and Lee, 1978; Saini et al., 1988; Sherif et al., 1989; Sharma and Sharma, 1997; Tyagi et al., 1998), lignin (Southerton and Deverall., 1990), chitin (Grinchenko and Chkanikov, 1989), esterase and β-glucosidase (Rebordinos, 1989; Chigrin et al., 1989; Ma et al., 2000), glutamine (Shrivastava and Chawla, 2001), polyamine and ornithine decarboxylase (Foster and Walters, 1992), glucose, fructose and invertase (Heisteruber et al., 1994) and ribonuclease activity (Chakravorty et al., 1974). Tyagi and Khanna (1987) observed that in powdery mildew resistant wheat varieties, the contents of soluble proteins were reduced, while there was a 2-3 fold increase in peroxidase and polyphenol oxidase activity. Molecular techniques like RAPD, RFLP, RGAP, AFLP and STS are some of the atest techniques being extensively used for the identification of alien chromosomes and segments in wheat background (Koebner and Martin, 1994; Schachermayr et al., 1994, 1995; Autriique et al., 1995; Bonhamme et al., 1995; Feuillet et al., 1995; Sun et al., 1997; Chen et al., 1998; Naik et al., 1998; Arumugam and Reddy, 1999b; Peng et al., 1999; Robert et al., 2000; Shi et al., 2001).