Journal of Wheat Research 2(1) : 7-19 (2008)

Prospects of hybrid wheat research in India

SK SINGH, DHARMENDRA SINGH, RAVISH CHATRATH & B MISHRA

Directorate of Wheat Research, Karnal-132001

ABSTRACT

Based on the results and experiences in Indian hybrid wheat programme, it was concluded that out of two pollination control systems (CHA & CMS), the cytoplasmic genetic male sterility system, though cumbersome, provides useful and eco-friendly approach for hybrid seed production. The CHA approach indicated certain inherent problems beyond control and, therefore, not found practically feasible to produce hybrid seed. Besides, the CHA system was effective to attempt large number of hybrid combinations and preliminary testing of these hybrids on multi locations. The multi locations and multiyear data revealed that only few hybrids performed well. The parents of these superior hybrids might be used as basic material for CMS line development and restorer conversion. The *timopheevii* based CMS system was found most appropriate since the fertility restoration was highly satisfactory.

Key words: Hybrid wheat, CHA, CMS, Fertility restoration

GLOBAL WHEAT PRODUCTION SCENARIO

At global level, India ranks as second largest wheat-producing nation and contributes approximately 11.7% to the world wheat production from about 12% of global area (USDA, 2007). China is the largest producer of wheat with 17.6% global wheat production from about 11% area under wheat. The other major wheat producing countries are the United States of America, the Russian Federation and Australia and these five countries together contribute more than half of the global wheat production.

Major wheat growing countries and their production (mt)

	Country	2003/04	2004/05	2005/06	2006/07	2007/08*
1	China	86.49	91.95	97.45	104.47	106.00
2	India	65.10	72.15	68.64	69.35	74.89
3	USA	63.81	58.74	57.28	49.32	56.25
4	Russia	34.10	45.40	47.70	44.90	48.00
5	Australia	26.13	21.91	25.37	9.90	13.00
6	Canada	23.05	24.80	25.75	25.27	20.60
7	Turkey	16.80	18.50	18.50	17.50	15.50
8	Argentina	14.50	16.00	14.50	15.20	15.50
9	Iran	13.50	14.50	14.50	14.80	15.00
10	Kazakhastan	11.00	9.95	11.00	13.50	16.00
	World	554.42	626.83	621.66	593.66	602.31

Estimations in Dec 2007

The area under wheat throughout the world as well as in India has become nearly constant around 215 m ha and 26 m ha, respectively. The enhanced genetic potential of new genotypes by introducing the semi-dwarf, photoperiod insensitive and fertilizer responsive varieties and increased area under cultivation during Green revolution era resulted in the increased productivity as well as production in India @ nearly 1% per annum. After green revolution the veery genotypes developed with 1B-1R translocation kept on increasing wheat yields in the country but the average production level is hovering around 70 m tones during last decade with average productivity of 2.7 t/ha. As per present population growth rate, population of India will be around 1.3 billion by 2025 AD. Assuming 20% more per capita requirement of food grains, due to better standard of living and increase in the demand of processing industries, required wheat production will be around 109 mt by the year 2025 AD (DWR 2007).

SCOPE AND IMPORTANCE OF HYBRIDS

The wheat growing areas in the country has been divided into six mega zones based on the agro-ecological conditions. These are northern hill zone (NHZ), north western plains zone (NWPZ), north eastern plains zone (NEPZ), central zone (CZ), peninsular zone (PZ) and southern hills zone (SHZ). Among these, the north western plain zone (NWPZ) was the seat of green revolution and contributed maximum to the wheat basket of the country. Presently, it is being felt that this major wheat producing zone of our country comprising Punjab, Haryana, western UP and parts of Rajasthan has reached a sort of saturation level. Against the projected demand of 109 m tones by 2025 AD with productivity growth rate of 2.1% per year, India can harvest over 95 m t of wheat merely by bridging the present level of yield gap between the realized and potential yield as demonstrated through frontline trials especially in north eastern plains zone comprising of eastern UP, Bihar, Jharkhand and west Bengal and in central zone with areas of MP, Chattisgarh, Gujrat and parts of Rajasthan and UP. Thus, there is need to explore new innovative approaches in order to break the yield barriers and make wheat cultivation more remunerative. In this context, exploiting hybrid vigour at commercial level through development of hybrid wheat is considered promising. Work on hybrid wheat started world over in 1962 and utilization of heterosis through hybrid breeding has given very high dividends in many field crops including horticulture.

The floral biology of wheat ensures that it is a 100 per cent self pollinated crop with occasional out crossing of usually less than 1 per cent. Consequently, selection for floral characters which enable sufficient cross fertilization like more open flowering habit, duration of flower opening, improved anther extrusion in the male parent and stigma receptivity in the female parent is crucial for successful development of hybrids. The discovery of an effective cytoplasmic male sterility and pollen fertility restoration systems in wheat opened up new avenues for commercial hybrid seed production. Kihara (1951) pointed out the possibility of using male sterility by transferring the nucleus of common wheat into the cytoplasm of *Aegilops caudata.* Among the cytoplasms which in an interaction with *Triticum* nucleus bring about sterility, *Triticum timopheevii* seems to be the most suitable one for commercial production of hybrid seed. The economics of hybrid seed production is of major concern for successful hybrid technology. The contributing factors such as the plant population, male and female row ratios, plant spacings and input managements should be optimized for getting maximum hybrid seed at lower costs.

A BRIEF HISTORICAL SURVEY OF HYBRIDS OF WHEAT

The research and development of hybrid wheat has a long history. Although the principal work has taken place during the 50 years beginning in 1950, the concept has been strongly influenced by developments in the production of line varieties of wheat over a longer period and by experience with hybrids of other species.

A CHRONOLOGY OF EVENTS RELATED TO HYBRID WHEAT DEVELOPMENT

1909 : Hybrid maize first proposed by Shull

1912 : The over-dominance theory of heterosis proposed by East and Hayes

1917 : The dominance theory of heterosis proposed by Jones

1919 : Heterosis was first reported in wheat by for plant height (Freeman)

1934 : Heterosis first reported in Wheat for yield (Engledow and Pal)

1951 : Cytoplasmic male sterility introduced into wheat using Aegilops caudata cytoplasm (Kihara)

1953 : Studies of the effect of maleic hydrazide as a chemical hybridizing agent (CHA) published

1957 : USA is the first country to plan hybrid wheat production

1958 : CMS research started on wheat in Kansas

1959 : Nuclear male sterility reported in Wheat (Pugsley and Oram)

1961 : Fertility restorers found in adapted wheat varieties

1961 : DeKalb Agricultural Association begins the first commercial hybrid wheat breeding programme

1961 : The variety 'Gaines' becomes the first semi-dwarf wheat to be released in the USA

1961 : Fertility restorers found in adapted wheat varieties

1962 : Source of CMS found in Triticum timopheevi (Wilson and Ross)

1962 : First commercially feasible CMS system proposed

1966 : McDaniel and Sarkissian proposed the theory of mitochondrial heterosis

1970 : British Hybrid Cereals formed by Rothwell Plant Breeders and Rank Hovis McDougall to exploit hybrid wheat and barley

1971 : DeVries commences publishing papers dealing with the suitability of wheat for cross-fertilization

1971 : Rohm and Haas begin CHA research

1972 : 'XYZ' system proposed for the utilization of NMS (Driscoll)

1973 : First feasible CHA discovered by Rohm and Haas

1974 : First commercial CMS hybrid wheat released in USA

1975 : Shell begin CHA research

1977 : Experimental evidence adds further doubt to the theory of mitochondrial complementation

1980 : The CHA WL 84811 discovered by Shell

1981 : Hybrid wheat varieties released by Cargill in the USA and by DeKalb in Australia

1982 : Monsanto starts HW program in US and Europe based on CHA Genesis

1982 : New CMS wheat hybrids make an impact on US market

1982 : Renewed interest in hybrid wheat in Europe follows signs that Rohm and Haas and Shell CHAs are satisfactory

1982 : Procedures for the official testing of hybrid wheat varieties published in France

1984 : OECD begins work on international certification scheme for hybrid wheat

1984 : Hybrid wheat varieties enter registration trials in the UK

1986 : Hybrid wheat varieties released in Argentina by Cargill

1988 : The CHA WL 84811 withdrawn after toxic residues found in F1 seed

1990 : Cargill cease production and sale of hybrid wheat in the USA, but continue commercialization in Australia and Argentina

1995 : ICAR (DWR) initiated work on Hybrid wheat in a network mode through CHA and CMS approach

2000 : Monsanto Co. stops GENESIS-based Hybrid Production and HW Activities in US and Europe

2002 : Dupont / Hybrinova stops Croisor-based Hybrid Production and HW Activities in Europe

It is noteworthy that work on hybrid wheat has been carried out in the majority of countries with significant cropping areas of this cereal. Major programmes of research have been run in many countries including Australia, Bulgaria, Canada, China, France, Germany, Hungary, India, Italy, Japan, Mexico, Netherlands, Pakistan, UK, USA, USSR and Yugoslavia. Hybrid wheat has been attractive to countries where wheat is an important crop. Production estimates for conventional wheat which show that in 1990, the above 17 countries produced approximately 80% of the world's wheat. Although the view has been expressed that hybrid production, in general, appeals to commercial interests, in most of these countries, hybrid wheat research was carried out in the public sector with work in the commercial sector apparently in second place.

EXTENT OF HETEROSIS

The basic requirements for the hybrid development are commercially-viable seed production system and levels of heterosis. It is well known that many characteristics related to performance may exhibit heterosis. Performance in terms of grain yield is a result of a complex of contributory factors involving many loci. Stroike (1987) suggested seedling vigour, improved root system, disease and insect resistance, adaptability, increased yield and improved milling and baking characteristics as six possible factors to heterosis in wheat. Commercial feasibility of a hybrid depends upon the heterotic advantage over the best ruling variety of that agro-climatic zone. High heterosis over mid and / or better parent was reported in wheat by several workers. Heterosis was first reported in wheat by Freeman (1919) for plant height. Since then many workers have observed heterosis for various traits in wheat. Reports have provided ample evidence of significant and positive heterosis over better parent for yield ranging from 0 to 100% in wheat (Briggle, 1963; Borghi and Perenzin, 1994; Larik *et al.* 1995; Wang *et al.* 1997 and Singh. 2003) but most of them are based on space planted and small plots. The heterosis over better parent for yield was noted to range from -40.62 to 29.75% among the winter x spring wheat (Chaudhary *et al.* 1993). They reported that the higher yielding parents from different eco-geographical regions produced high heterosis and favoured the hybridization between winter and spring wheats. Harvest index is an important indicator of source to sink relationship and therefore, Kumar and Ganguly (1993) advocated the possibility of increasing yield potential through better harvest index. The development of F1 hybrid varieties of wheat was recently reviewed by Pickett and Galwey (1997). They also supported the hypothesis that heterosis in wheat arises from dominance with the additional factors of linkage and interaction of alleles. Under the field conditions, the minimum accepted standard heterosis for yield is 20% for commercial exploitation of a hybrid. Significant standard heterosis of more than 20% was observed for yield and yield traits under drill sown conditions (Singh *et al.* 1997 and Zehr *et al.* 1997).

FLORAL BIOLOGY

Floral structure, anthesis and anther dehiscence patterns in wheat make this crop strictly autogamous (Percival 1921; Leighty and Sando 1924). De Vries (1971) reviewed the floral biology of wheat keeping in view the possibility of hybrid seed production. For hybrid development, adequate cross pollination attributes are the necessity. The occurrence of outcrossing in wheat and the tendency for some cultivars to outcross more than others was well established (Griffin 1987). Around six decades ago, Leighty and Taylor (1927) demonstrated that outcrossing occurred more frequently in late emerging spikes of wheat cultivars. The extent of natural outcrossing in cultivated varieties of wheat was observed to be 0.0 to 6.05 per cent (Heyne and Smith 1967; Martin 1990; Hucl 1996 and Singh 2006). A positive correlation of outcrossing with length of flowering period was observed (Martin 1990). Mixed chasmogamous / cleistogamous type of flowering and autogamous / allogamous mode of pollination in wheat was observed (Chelak 1989; Chhabra and Sethi 1991).

Important floral traits that influence outcrossing in wheat are stigma size, anther size, anther extrusion, pollen number and pollen viability. The stigma length of wheat genotypes has been noted to be 2.13 – 5.2 mm (Percival 1921; Komaki and Tsunewaki 1981 and Singh 2005). Anther length has also been investigated by a number of workers and the range was observed from 3.0 mm to 5.09 mm. Anther extrusion, an important feature in wheat, has been observed from 14.1 to 93.0% (Singh and Joshi 2003). Phenotypic differences among wheat cultivars for days to heading and anthesis, anther extrusion, anther size, pollen grain size and pollen viability, stigma length, duration of floral opening and openness of florets were also observed by Chowdhary *et al.* (1994); Singh and Joshi (2003) and Singh *et al.* (2007). They also suggested that the selection for long anthers, high rate of anther extrusion and more openness of florets may be effective in promoting natural cross pollination. The pollen viability in wheat ranged from 81-98.6% (Hucl 1996; Singh and Singh 2001). In general, flowers of wheat reach their peak opening between 9.00 and 11.30 a.m. on a sunny day. Subsequently, a second flush of flower opening occurs between 15.00-17.00h (Virmani and Edwards 1983). The largest separation angle between the glumes of first two florets of spikelet was observed to be 16-400. Wheat florets get closed within 12 – 20 minutes of flower opening with extreme values being 8 and 39 minutes (Singh and Singh 2004). Gorin (1968) observed 80-90 per cent open florets in most of the bread wheats. Flowering continues throughout the day, with 2-6 days required for a spike to finish blooming. After the first round of blooming, unfertilized florets open again, exposing the stigma for another 2-3 days with the ovaries remain receptive for an additional 2-3 days (Hoshikawa 1960). Likewise, in male sterile plants the second round of flowering starts 36 hours after the first round and florets remain opened for another 5 days (Molnar-Lang *et al.* 1980).

There is a positive association between anther size and the quantity of pollen produced per anther (Beri and Anand 1971). Furthermore, within wheat cultivars, a large variation is reported for the number of pollen grains produced per anther. Under optimal field conditions (20°C, 60% RH), wheat pollen is viable for approximately half-an-hour (D' Souza 1970; De Vries 1971). All the viable pollen grains that have access to the stigma surface germinate as soon as they come in contact with the stigma (Chandra and Bhatnagar 1974). Because the entire length of stigma receptive to pollen grains in wheat, the location of pollen landing on stigma, does not affect pollen germination. Stigmas are receptive for 2 to 13 days after anthesis, and are most receptive for the first 2-5 days (De Vries 1971). Amount of out crossing may be increased by a larger stigmatic surface and longer style exertion. The angle of separation between the lemma and palea is important in such a way that both the branches of the stigma protrude from the floret during flowering. Wheat pollen is relatively heavy compared with other grasses pollen and travels 1m from the pollen source (Lelley 1966).

MALE STERILITY SYSTEM IN WHEAT

Wheat is monoecious and therefore a line designated as female must not be allowed to produce pollen capable of fertilisation whilst acting as a parent. It must, however, be able to do so for the maintenance of the line. Since wheat flowers are hermaphrodite, the labour requirement for mechanical emasculation is clearly prohibitive. Methods for procuring male sterility in plants may be divided into two groups on the basis of the role of the genotype. Systems involving the plant's genes include cytoplasmic male sterility, nuclear male sterility and self-incompatibility (Wricke 1989). On the other hand, there is no direct genetic involvement in chemical hybridization or hand emasculation. Different methods for obtaining male sterility namely cytoplasmic genetic male sterility (CMS), nuclear / genetic male sterility, chemical induced male sterility (CHA) and environmental male sterility have been proposed for wheat but CMS and CHA approaches are widely used in wheat as pollination control system.

1. CYTOPLASMIC GENETIC MALE STERILITY SYSTEM

This system is commonly known as CMS system and involves three types of parental lines namely, the male sterile line (A-line), the maintainer line (B-line) and the fertility restorer line (R-line). Hybrids are the resultant of A x R crosses. Although the CMS approach has advantages of complete sterility in female lines, absence of toxicity and chemical registration costs but it requires much pre-breeding, long term commitment of resources and labor and has slow process. Cytoplasmic genetic male sterility is visualized as an essential genetic tool to F1 hybrids in self pollinated crops.

1.1 SOURCES OF CYTOPLASMIC GENETIC MALE STERILITY

Kihara (1951) reported the cytoplasmically induced male sterility in wheat for the first time by substituting common wheat genome into *Aegilops caudata* cytoplasm. The possibility of hybrid wheat became apparent only when Wilson and Ross (1962) discovered another effective source of male sterility in *T.timopheevi*/ 'Bison' cross. Following the report of Kihara (1951) on *Ae. caudata*, Curtis and Johnston (1969) also observed *Ae. caudata* and *Ae. ovata* as good sources of cytoplasmic male sterility. A number of species from genera *Triticum* and *Aegilops* were reported as source of male sterility but *Triticum dicoccoides* var. *spontaneovillosum*, *Ae. aucherii* (Stehno and Apltaverova 1980, 1981); *T. zhukovskii* (Apltaverova *et al.* 1981); *Ae. ventricosa* (Zhang and Yang 1989) and *Ae. kotschyi* (Ushiyama *et al.* 1996). were considered as the good sources of cytoplasmic genetic male sterility. *Triticum timopheevii* was observed to be major source of male sterility in wheat by several workers (Curtis and Johnston 1969; Apltaverova *et al.* 1981; Il'ina 1985 and Ushiyama *et al.* 1996) and is now most widely used cytoplasm in hybrid wheat production.

1.2 FERTILITY RESTORATION SYSTEM

T. timopheevii and its derrivatives were also observed as potential source of fertility restoration system in wheat (Schmidt *et al.* 1962; Wilson 1972; Panayotov *et al.* 1986). Other sources of fertility restoration in wheat were wheat varieties Primpei (Oehler and Ingold 1966), Lal Bahadur, Ridley and HD1944 (Karim and Singh 1984), and related hexaploid species *T. dicoccoides* var. *spontaneovillosum* (Panayotov *et al.* 1986) and *T. spelta* var. *duhamelianum* (Kihara and Tsunewaki 1964).

1.3 GENETICS OF MALE STERILITY - FERTILITY SYSTEM

Two incomplete dominant genes with epistatic action were noted to control fertility-sterility system in wheat by Nettevich and Naumov (1970). A gene *ms2* for male sterility was observed on short arm of chromosome 4D by Liu and Yang (1994). Liu *et al.* (1996) reported that the male sterility was controlled by double recessive nuclear type action and suggested involvement of upto 2 genes, designated as fms1 and fms2 for male sterility. Single recessive gene was also found responsible for male sterility (Il'ina 1984; Chhuneja and Minocha 1993).

Fertility restoration in wheat has been reported to be under the control of monogenic, digenic as well as polygenic control. The complexity of the genetics of restoration is evident from the fact that restorer genes are carried on many chromosomes in wheat (Sage 1976). These include chromosomes 1, 2, 5, 6 and 7.

Three genes, located on chromosome 1A, 6B and 7D of *Triticum-timopheevii* were found responsible for complete fertility restoration (Wilson 1972). However, Ralko (1982) observed all the three (monogenic, digenic and polygenic) mode of inheritance. Chromosome 1B of Chinese Spring was also identified as carrier of fertility restoration gene (Tsunewaki 1982; Tsujimoto and Tsunewaki 1984). El-Kadi *et al.* (1983) observed 2-3 major genes in R line for fertility restoration while two dominant (Gotsova *et al.* 1987) and two additive genes (Wrobel 1989) were found responsible for fertility restoration. Multiple recessive genes with minor effects were responsible for control of fertility restoration in wheat (Murai *et al.* 1995). Ma *et al.* (1991) observed that atleast one gene is responsible for controlling fertility restoration in wheat. On the other hand, Du *et al.* (1991) reported that two genes, responsible for fertility restoration, (*Rf1* and *Rf4*) were located on chromosome 1A and 6B, respectively. Ikeguchi *et al.* (1994) observed the location of fertility restoration gene *Rfv1* on chromosome 1B.

Cytoplasmic male sterility and male fertility restoration systems in hexaploid wheat are conditioned by interaction involving dosage of *Rf* genes (restoration of fertility) and *Fi* genes (Fertility inhibiting) in polyploidy nucleus and Cytoplasmic genes of the related alloplasmic species. The plant vigour restoring genes *Vi* also play important role. Function of *Rf, Fi* and *Vi* were not mutually exclusive and same genes may have produced different genotypes in combination with different cytoplasm and wheat nuclear genes (Mann 1992). More than 10 different Rf genes have been reported (Kucera 1982; McIntosh and Cusick 1987: Huang 1990: Chen *et al.* 1998). The adequate fertility restoration of R-lines to T-type CMS needs more than two doses of these *Rf* genes. Stable, complete fertility restoration needs even more (Huang 1990; Chen *et al.* 1998). Although fully self-fertile alloplasmic lines with homozygous *Rf* genes are easily obtained, most of the hybrids with the CMS lines are not fully fertile. The problem also remains in other alloplasmic wheats such as the K-type (with cytoplasm of *Ae. kotschyi*) and the V-type (with cytoplasm of *Ae. ventricosa*) hybrids. To improve the male fertility restoration of common wheat for *T. timopheevii* cytoplasm, Chen (2003) proposed the new model of A-line/R* line// R-line in the production of hybrid wheat.

1.4 EFFECT OF CYTOPLASMS

Different sources of male sterility system carry their own negative effects on growth and productivity of wheat. The cytoplasm from *Triticum timopheevii* has been found to exhibit tendency towards pistiloidy and meiotic instability, reduced dry matter weight, kernel shriveling, low seed germinability, higher anther extrusion, increased tiller production and ear length, decreased grain weight/ear and reduced grain filling by several workers. The *Aegilopes* cytoplasms were also found to express delayed heading, reduced plant height, longer ears, more productive tillers/ plants and shrivelled grains when crossed to maintainer/ restorer line owing to late maturity. Zhang and Yang (1989) found that *Ae. ventricosa* cytoplasm gave rise to stable sterility and normal seed plumpness of male sterile F1s and F2s and did not result in harmful maternal effects.

1.5 BREEDING SCHEME FOR HYBRIDS USING CMS

The CMS system for producing hybrid seed has been described many times (Rodriguez *et al.* 1967; Sneep *et al.* 1979; Wilson 1984 and Kaul 1988). In this system, the production of a single cross hybrid requires three lines, two to provide a female parent and one for the male. On the female side, after a genotype has been selected for combining ability, the first requirement will be to transfer it to a sterilising cytoplasm. In most species, CMS is incorporated into a line of the female parent by backcrossing using the line with the male sterile cytoplasm as the recurrent parent and the normal, male fertile line, as the donor parent (Newton 1988). The CMS line is, by convention often designated the 'A' line. Workers vary on the subject of the number of backcrosses required to produce a CMS line: Zeven (1967) states six (taking three years); Macer (1972) eight, Tsunewaki *et al.* (1980) ten, Bingham and Lupton (1987) five. Although it is possible for CMS lines, once developed, to remain true to type, problems are sometimes experienced in the maintenance of sterility. Wilson (1968b), for example, confirming that male-sterile 'Bison' had been multiplied successfully through 14 generations, noted some exceptions in other lines.

A line carrying the same nuclear genotype in a fertile cytoplasm, usually from *T. aestivum*, is used for pollinating the A line for maintenance purposes. This line is known as the 'B' line. The preservation of CMS relies on the non-transmission of the cytoplasm by the pollen of the male. The male parent, in addition to being selected for combining ability, must normally carry genes to restore fertility to the F1 hybrid. Restorer genes are incorporated into the male parent by means of a crossing programme, which may also include backcrossing. Restorer genes are given the designation 'Rf' and it is customary to denote the restorer as the 'R' line. In wheat, the B and R lines are both maintained as normal inbred lines, without difficulty, using conven¬tional seed production arrangements. The restorer locus or loci will be heterozygous in the FI hybrid. Segregation will, therefore, take place in subsequent generations, precluding the use of CMS in the production of F2 hybrids of wheat. The following diagram describes the basic system for producing an FI hybrid by means of CMS. This uses the commonly adopted notation whereby the CMS is termed the' A line', its maintainer with the same nuclear genotype is called the 'B line' and the restorer acting as the male parent of the Fl hybrid is the 'R line'.

2. CHEMICALLY INDUCED MALE STERILITY

The limitations of cytoplasmic male sterility system, viz., unstable nature, undesirable linkages and need for use of maintainers have prompted breeders to develop simple and more efficient methods to create male sterility by other means like use of chemicals, mutagens for induction of male sterility. Male sterility induced by chemical hybridizing agents is relatively more convenient to use because there is no need to maintain it does not require any pre-breeding, fast and relatively easy to implement and many and virtually any combination can be explored. Besides, it has disadvantages of very expensive to develop and register, highly crop growth stage-dependent and weather-dependent, often non-complete sterility in female and somewhat phytotoxic effects. Compared with CMS systems, an effective CHA allows the production of large numbers of parental combinations and permits the evaluation of a number of inbreds for combining ability and/or breeding value. This substantially reduces the time required for hybrid development. More than 40 chemicals have been patented as potential CHAs world over out of which etherel and maleic hydrazide are most commonly used. Complete male sterility by spraying of etherel at early stem extension stage was observed along with reduction in plant height due to reduced internode length, plant development, yield and increased number of fertile tillers. The Shell compound WL84811 and the Monsanto CHA "GENESIS" are well known current generation of CHAs for inducing male sterility. The appropriate stage for higher efficacy of CHA was observed at spike length of 7-8 mm to early boot stage and the late sown crop was found more responsible to CHA than normal sown crop. The hybrid development process via CHA route involves the induction of male sterility in female lines through chemical spray at appropriate stage and the pollination for seed set.

Attributes of an ideal CHA have been suggested by several authors including Liable (1974), Virmani and Edwards (1983) and Pickett (1993). A collective list of those attributes for an ideal CHA includes:

Selectively induces only male sterility with no effect on female fertility

Produces male steriles that are readily apparent

No phytotoxic effect on the treated parent Effective on all genotypes of a species

Effective in a wide range of environments

Has systemic activity or persistence to sterilize early and late tillers or plants in the field population

Has flexibility in time of application to overcome adverse weather effects and to permit treatment of many hectares

Has considerable dosage flexibility to permit a safety margin for application

Achieves sterility with a single treatment

Does not adversely affect F1 seed quality, or F1 seedling or plant vigour

Effective on several genera

Economical to synthesize and practical to apply

Safe and non-toxic to the environment

While there are a rather large number of chemicals that cause male sterility in wheat, there are very few that meet most of the above requirements. Once a chemical is identified as having some CHA activity, much work needs to be done to identify the optimum time and rate of application. Additionally, application rates can vary with environment and genotype and can be modified with the use of chemical surfactants.

3. GENETIC MALE STERILITY

A number of genes have been identified which prevent the production of pollen capable of fertilisation. It is possible for male sterility to be achieved without a significant reduction of female fertility. Since most normal wheat varieties will act as restorers of fertility, necessary for the Fl plant, it is only necessary to breed special female parents. Genes controlling nuclear male sterility fall into two categories: those showing dominance or near dominance for sterility and those which are recessive. Fertility in plants is usually encoded by dominant genes. Mutations of a single gene are the probable cause of the majority of examples of Nuclear / genic male sterility in plants. These may cause an alteration of a gene to the recessive state leading to loss of function and sterility. Except in special circumstances, reces¬sive genes for male sterility are highly desirable because they usually facilitate identification of homozygous sterile progenies for Fl production. However, it is unlikely that the all NMS genes act in the same way. Some, for example, act as dominants. There have been many reports of genetic male sterilty (GMS) of wheat that advocated that five GMS loci have been located to chromosomes so far. These loci are

ms1, a recessive gene located to chromosome arm 4BS ;

Ms2 and *Ms3*, two dominant genes located to chromosome arm 4DS and 5AS respectively;

Ms4, a dominant gene located to chromosome arm 4DS and

ms5, a recessive gene located to chromosome arm 3AL.

Wilson (1984) noted that, despite very full investigations, GMS had not been utilised commercially for cereal crops. Apart from use in China, there is little to suggest that GMS has yet reached commercial use. The basic requirement for the GMS system is the existence of genes encoding male sterility. The drawback with most systems is large scale production of uniformly sterile seed. There is much work to be done before this method of producing male sterility could be used. GMS, however, offers certain potential benefits including the absence of the need for special restorer varieties and reasonable freedom from the damaging side-effects apparent in many forms of CMS. Most conventional varieties of wheat may be used to for this purpose, making it possible to select male hybrid parents from a wide range of varieties. The disadvantage of GMS wheat was the maintenance the male sterile line. In general, this requires production of a population heterozygous to at the locus controlling fertility. The fertile segregants must then be removed from the hybrid seed production field prior to flowering. Although a marker gene linking to a conspicuous morphological character to fertility could, in technical terms, allow removal of the male fertile plants, in practice, the scale of operations would preclude this approach. It is possible that new techniques could find application in developing GMS. For example, if it becomes possible to manipulate cereal genes directly, it may then be possible to complete the assembly of a workable system. It may, however, be more worthwhile to attempt to link a gene for herbicide tolerance to male sterility to provide the means to remove fertile segregants in an NMS line.

4. ENVIRONMENT SENSITIVE MALE STERILITY (EMS)

The male sterility induced by change in environmental conditions are also investigated as tools for developing wheat hybrids following two line breeding methodology. These included photoperiod-sensitive cytoplasmic (Murai and Tsunewaki 1995), photoperiod sensitive genetic (Fisher 1972), temperature-sensitive genetic (Jan 1974; Qian *et al.* 1986) and micronutrient deficiency-induced male sterility (Agarwala *et al.* 1980; Rerkasem and Jamjod 1997). Since these techniques are the alternate approaches for inducing male sterility, the investigations for their effective utilization are still going on.

Commercial Hybrid Seed Production

The most important requirements of cross-fertilization and hybrid seed production are:

Flowers must open at peak flowering period

The stigma must be receptive to accept the pollen from male

Anthers must release pollen outside the flower by good anther extrusion

The slight wind must be present to carry the heavy pollen from male to female plants

Pollen must be viable till fertilization.

Two constraints apply to hybrid seed production in wheat. First, the multiplication rate of the species is naturally low. Second, as cross-fertilization may frequently be inefficient, leading to low levels of seed set. In the hybrid seed production field, it is necessary to maintain careful separation of male and female parents. If this is not achieved, the hybrid seed will be contaminated with parental lines and unwanted hybrids. In view of the poor transportation of pollen, the distance of separation of parents must, however, be the minimum consistent with the cost-effective use of farm machinery. Where a CHA is used, it is, of course, necessary to perform an accurate application of the chemical without leaving the female parent male fertile or treating the male parent. Amongst the more important characteristics benefiting hybrid seed production in wheat, a consistent climate with warm and sunny conditions without excessive rainfall is needed. However, excessive heat may be harmful. If production is to be carried out away from the area of use, parental varieties will have to be selected to synchronize in the production environment. It is also apparent that the environment within an area can, to a degree, be optimized for wind pollination by choice of a field exposed to wind and by aligning the beds in such a way that the prevailing wind can move pollen from the male parent to the female.

Investigations concerning male: female ratio for hybrid seed production of wheat have demonstrated yield advantage at variable ratios. Wilson (1968) reported 70% seed set in 1:1 ratio of the sterile and pollinator parents but suggested the possibility of profitable management of 2:1 ratio. Maximum yield at 1:1 ratio of male sterile / pollinator parent followed by 2:1 and 3:1 ratio in production / hectare basis was observed by Miller and Lucken (1976). However, female: male row ratio of 2:1 or 3:1 was also reported for getting maximum seed set (Singh and Singh 2006). Araki (1990) observed 0-80% grain set in male sterile line and reported higher seed setting when male sterile line headed 5-10 days before the restorer lines. He also observed a close relation of seed set with extent of synchrony in heading of maternal and pollen parent. A direct effect of cross-fertilisation on seed yield and the cost of hybrid seed were also reported.

HYBRID WHEAT RESEARCH AT CIMMYT

The work on development of hybrid wheat was started in 1962 at global level in many countries. Ing. Riccardo Rodriguez initiated the research efforts at CIMMYT in 1962. The elite CIMMYT lines were transferred with T. timopheevi cytoplasm, the fertility restorer (*Rf*) genetic stocks were developed and the experimental hybrids were produced and evaluated but the advent of semi dwarf high yielding wheat varieties, the emphasis got further strengthened only to popularization and genetic improvement of pure line varieties and as a result the research efforts on hybrid wheat got distracted. The work was discontinued as no significant results of heterosis were observed for commercial exploitation.

The research efforts were readdressed at CIMMYT during 1997-2002 in collaboration with the Monsanto Co. with the objectives to develop a practical hybrid wheat production scheme in Northern-Mexico, based on the GENESIS (CHA) technology and to identify spring hybrid bread wheats with superior Yield potential, leaf-rust resistance and acceptable quality, under optimal conditions. In these efforts, the doses and crop stage were optimized for complete male sterility, the female-sterility was monitored and adequate levels of male-sterility were achieved with GENESIS on experimental scale. The weather survey was made to identify suitable locations in Mexico and pilot seed production experiments were conducted at various locations. In the studies, the acceptable female-sterility levels were observed along with low seed-set in general, commercially unviable and variable results with locations. These findings were concluded that the heterosis is present at moderate to low levels. The good combining male and female backgrounds were identified. In addition, the heterotic pattern in CIMMYT lines was identified and the whole germplasm was divided into two distinct heterotic groups. After these, the work on CHA based hybrids or on hybrid development was discontinued at CIMMYT.

INDIAN EFFORTS ON HYBRID WHEAT DEVELOPMENT

In 1995, Directorate of Wheat Research, Karnal has addressed the hybrid wheat development through CMS and CHA approach in network mode. Through CMS approach, cytoplasmic male sterile lines were developed by using *Triticum timopheevi*, *T. araraticum*, *Ae. caudata* and *Ae. Speltoides* as source parents. No apparent adverse effects on morphology by *T. araraticum* and *Ae. speltoides* have been noticed. Two exotic genetic stocks registered as PWR 4099 and PWR 4101 indicated complete fertility restoration in *T. timopheevi* based CMS lines. Although there is no significant result for heterosis for yield in totality, few hybrids showed heterosis for yield components viz. spikelet number, spike length and tillers/plant. Through CHA approach, chemicals were identified that induced male sterility when sprayed at 10-15mm of spike length at 50-60 days after germination in most of the genotypes (Mahajan *et al.* 1997). Over 1500 single cross hybrids developed through CHA were evaluated of which, 6 hybrids were identified depicting standard heterosis over the best check and superior quality parameters. After thorough experimentation, 2: 3 row ratio of male and female was found most suitable for higher seed production. The profuse growth habit of 'oat' is used as space isolation to separate the various combinations of hybrid plots to avoid contamination from non parental male genotypes. The supplementary pollination through rope pulling during the peak hours of flowering in both morning and after noon was suggested for enhanced out crossing. An "Improved DWR CHA spray system" was also fabricated for large scale hybrid seed production which has précised delivery of CHA with coverage rate of one acre per hour. Besides, a seed sowing drill was also fabricated for simultaneous sowing of male and female parents for hybrid seed production.

FUTURE STRATEGIES OF HYBRID WHEAT RESEARCH

For a successful breeding programme and commercially viable hybrid seed production, following criteria are required:

The hybrids must satisfy the needs of the customer for all important traits. Simply to be "hybrid", or simply to exhibit "heterosis", is not enough.

The price of hybrid seed must be low enough to enable the customer to make substantial profits from annually recurring investments in expensive hybrid seed. A rule of thumb is that a first time use of hybrid seed should enable the farmer to earn an extra profit equal to at least three times the added cost of the seed.

The price of hybrid seed must be high enough to enable the seed producer to make substantial profits from its investments in research, production, and sales.

To satisfy these primary criteria for success in the hybrid seed business, the organizations involved in hybrid development programme must integrate a host of variables such as:

The pollinating system of the crop

Options for manipulation of the pollinating system

Supply and cost of labour for emasculation / other requirements for hybridization

The yield of the crop in the farmer's field

The commercial value of the crop per unit of land area

The seeding rate of the crop

The seed yield in the seed production field

The extra yield to be expected from heterosis

The implications of hybrid uniformity

The most important traits to improve in the crop, and their genetics

The ease of demonstrating improvements in new hybrids and

Availability of inbred parents and other breeding materials in either public or private institutions.

Wheat hybrids can yield up to 30% more than their parents, but hybrids with heterosis at these levels usually are the product of crosses between different classes of wheat, such as a cross of hard red winter wheat by soft red winter wheat. Commercially useful wheat hybrids must be made within a class, to maintain milling and baking quality. Crosses within a quality class typically have less heterosis, only about 5-15% more than their parents. The lower amount of heterosis may be because of relationship among members of a relatively closed gene pool. The experiments indicated that the heterosis level should be minimum of 20% over the best check of the area for its commercial viability. As wheat is a self-pollinated crop, it has perfect florets, limited supplies of pollen, and a relatively brief period of stigma receptivity, the hand emasculation is impractical for commercial production of hybrid seed, but cytoplasmic male sterility allows production of hybrid wheat seed on a field scale. Limited pollen production by male lines as comparied to maize, for example means that the ratio of male rows to female rows must be relatively high, and seed yield per hectare is reduced correspondingly. If a hybrid has only a small yield advantage over the best pure line cultivars, the expected gain in the farmer's income from increased yield of the hybrid could be less than the cost of the hybrid seed, hence such a hybrid would be unacceptable, despite its yield advantage. Breeders had to develop entirely new male lines, by inserting nuclear genes for fertility restoration into non-restorer genotypes. Restorer lines usually were made by introgressing dominant fertility restorer genes from widely divergent germplasm into elite wheat lines. Typically, the strongest and most useful restorer genes came from different species, sometimes weedy or wild species. This introduced problems of linkage to undesirable traits from the alien species. Breeders devoted years of time and energy to backcrossing with selection for strong fertility restoration, and, as a consequence, spent less time on breeding for increased yield and general performance. Also the public wheat breeding programmes provides very little input to hybrid wheat breeding in terms of investment. This led to under-investment in development of germplasm and breeding methods (particularly for restorer males) in the important start-up period.

Interest in hybrid wheat is still present particularly in regions where wheat yields and commercial value of the crop are relatively high (Edwards 1997). However, the hybrids are planted at very low seeding rates, thus keeping seed cost in line with expected return. Research is in progress in several organisations on new ways to produce hybrid wheat seed, using new sterility systems, some of which are introduced into wheat via genetic transformation. The goal is to build systems that are reliable, easy to manipulate, and that interfere as little as possible with routine wheat breeding programs aimed at making improvements in yield and general performance. These show that breeders still believe that hybrid wheat can succeed on large scale, and perhaps more importantly they show that there are numerous ways to produce the hybrids, and then to manage them for profit in the farmers' fields.

As the Directorate of Wheat Research is nodal centre for wheat research and coordination in the country, it addressed the hybrid development programme through CMS system in network mode with cooperating centres in four major wheat zones, i.e., NWPZ, NEPZ, CZ and PZ. As most of the available CMS lines are in exotic background, there is need to diversify them in indigenous background for exploiting better adaptability of superior agronomic backgrounds. Similarly, the fertility restoration is an important issue which needs identification of fertility restorer lines and their diversification. The identification of heterotic groups for diversification programme is pre-requisite for selection of diverse parents. As the level of heterosis is not commercially viable in most of the combinations, the future work needs for intra pool improvement of male and female parental lines separately through pre breeding approach so that the distinct heterotic pools may be obtained for realizing high heterosis levels. The search for open pollinating traits in diverse wheat germplasm lines and their exploitation and the standardization of the hybrid seed production technology for economic seed production are the areas of future efforts in the direction of development of a successful hybrid wheat technology. In nutshell, following points may be considered as future strategy for hybrid wheat development programme.

Identification of heterotic gene pools

Creation of novel genetic variability for yield component traits from secondary and tertiary gene pools and its evaluation

Improving the fertility restoration by accumulation of *Rf* genes

Use of variability available in dwarfing genes for parental diversity

Biotechnological tools for molecular interventions related to fertility restoration

Search for heterosis in diverse gene pools

Fixation of heterosis through apomixis

Understanding of floral biology

Promotion of active interaction between public and private organizations

REFERENCES

Araki H. 1990. Studies on the practical use of hybrid wheat using cytoplasmic male sterility. *Bulletin of the Kyushu National Agricultural Experiment Station* **26** (2): 115-165.

Agarwala S C, Sharma P N, Chatterjee C and Sharma C P. 1980. Copper deficiency induced changes in wheat anthers. Proc. *Indian Natl. Sci. Acad.Sect* **B2**: 172-176

Apltaverova M, Stehno Z and Dotlacil L. 1981. Cytoplasmic male sterility in wheat. *Vedeck'e Prace Vyzkumnho Ustavu Rostlinne Vyroby v Praze - Ruzyni* **21**: 29-52.

Beri S M and Anand S C. 1971. Factors affecting pollen-shedding capacity in wheat. *Euphytica* **20**: 327-332.

Bingham J and Lupton E G H. 1987. Production of new varieties: an integrated research approach to plant breeding. In: Wheat Breeding, its scientific basis. Ed: Lupton, E G H. Pub.: Chapman and Hall, London and New York. pp 487-538.

Borghi B and Perenzin M. 1994. Diallel analysis to predict heterosis and combining ability for grain yield, yield components and bread making quality in bread wheat (*Triticum aestivum L.*). *TAG* **89** (7-8): 975-981.

Briggle L W. 1963. Heterosis in wheat - A review. *Crop Sci.* **3**: 407-412.

Chandra S and Bhatnagar S P. 1974. Reproductive biology of Tritium. II. Pollen germination, pollen tube growth, and its entry into the ovule. *Phytomorphology* **24**:211-217

Chaudhary H K, Kapoor A S and Walia D P. 1993. Manifestation of heterosis in winter x spring wheat crosses, Short comm. in Symp. on Heterosis breeding in crop plants, P A U, Ludhiana.

Chelak V R. 1989. Type of flowering and mode of pollination/fertilization in wheat (*Triticum aestivum L.*). *Botanicheskie Issledovaniya* **4** : 11-30.

Chen Q F. 2003. Improving male fertility restoration of common wheat *Triticum timopheevii* cytoplasm. *Plant Breeding* **122**: 401-404.

Chen Q F, Zhou Y H, Peng Z S and Jiang H R.1998. Studies on the distribution of hybrid chlorosis *Ch1* gene and the T-type cytoplasm fertility restoring genes in Chinese endemic wheats. *Guihaiha* **18**: 325-330

Chhabra A K and Sethi S K. 1991. Inheritance of cleistogamic flowering in durum wheat (*Triticum durum*). *Euphytica* **55(2)**: 147-150.

Chhuneja P and Minocha J L. 1993. Induction of male sterility mutations in three cultivars of *Triticum aestivum* (L.). In. Heterosis breeding in crop plants theory and application; Short communications: Symposium Ludhiana, 23-24 February 1993 [Edited by Verma M M, Virk D S and Chahal G S, Ludhiana, India; Crop Improvement Society of India, pp. 130-131.

Chowdhary M A, Mahmood N and Khaliq I. 1994. Pollen production studies in common bread wheat. *Rachis* **11** (1/2) : 68-72.

Curtis B C and Johnston D R. 1969. *Hybrid wheat. Sci. Amer* **220** (5) : 21-29.

D'Souza V L. 1970. Investigations concerning the suitability of wheat as pollen donor for cross-pollination by wind as compared to rye, *Triticum, and Secalotricum.* (In German) *Z.Pflanzenzuecht* **63**: 246-269.

De Vries A P H. 1971. Flowering biology of wheat, particularly in view of hybrid seed production – a review. *Euphytica* **20**:152 -70.

Du H L, Maan S S and Hammond J J. 1991. Genetic analysis of male-fertility restoration in wheat. III : Effects of aneuploidy. *Crop Sci* **31** (2) : 319-322.

D W R. 2007. Vision 2025. pp.24

East E M and Hayes H K. 1912. Heterozygosis in evolution and in plant breeding. *United States Department of Agriculture, Bureau of Plant Industries Bulletin* **243**: 58.

Edwards I. 1997. Personal communication. Pioneer Hi-Bred International, Inc., Johnston I A, 50131 (USA). July 29, 1997.

Edwards I B. 2001. Hybrid wheat. In: Bonjean A P and Angus W J (eds), The World Wheat Book, a History of Wheat Breeding, 1017-1045. Lavoisier. Inc., Paris

El-Kadi D A, Hindi L H A, Gommaa A A and Ghazal H M. 1983. Analysis of male sterility in nine wheat hybrids with *T. timopheevii* cytoplasm. *Egyptian J. of Genet. Cytol* **12** (1) :1-15.

Engledow F L and Pal B P. 1934. Investigations on yield in cereals. VIII. Hybrid vigour in wheat. *Journal of Agricultural Science* **24:** 390-409.

Freeman G F. 1919. Heredity of quantitative characters in wheat. *Genetics* **4**:1-9.

Gorin A P. 1968. Results of studies on the biology of flowering and pollination in field crops. *Dokl. sel.-Khoz. Akad. Timiryazeva* **139**: 175-181 (*Pl. Breed. Abst.* **39**, 1969; 4289).

Gotsova D K, Panayatov I and Gotsov K. 1987. Male fertility restoration against various alien cytoplasms II. Genetical analysis of R-17127. *Wheat Inf. Ser* **64**: 1-5.

Griffin W B. 1987. *N.Z.J. Agric Res* **30** : 287-290.

Heyne E G and Smith G S. 1967. In "Wheat and wheat Improvement." (Quisenberry K S and Reitz L P, eds). pp 269-306. Amer. Soc. Agron., Madison, Wisconsin.

Hoshikawa K. 1960. Studies on the reopened floret in wheat. *Proceedings of crop science society of Japan* **29**:103-106.

Huang T C (ed). 1990. Studies on hybrid wheat-Progress, Problems and prospects. Publishing House of Beijing Agricultural University, Beijing, China.

Hucl P. 1996. Out crossing rates for 10 Canadian spring wheat cultivars. *Canadian J. Plant Sci* **76** (3) : 423-427.

Ikeguchi S, Hasegawa A, Oyamada Y, Toriyama K and Tsunewaki K. 1994. Basic studies on hybrid wheat breeding utilizing Aegilops kotschyi cytoplasm. In proceedings of the Japan-Russia workshop Sapporo on : low temp. physiology and breeding of northern crops, Sapporo, Japan, January 25-28, 1994. Hokkaido National Agricultural Experiment Station, 77-83.

Il'ina L B. 1984. Inheritance of genic male sterility in bread wheat. In Genet. selekts. issled. na Urale. Irf. materialy. Sverdlovsk, USSR, 48-50.

Il'ina L B. 1985. Investigating CMS in the process of producing sterile analogues of spring bread wheat. Ufa, USSR Rost I produktivnost rast. Dep. 2136- 85 : 15-32.

Jan C C. 1974. Genetic male sterility in wheat (Triticum aestivum L): Expression, Stability, Inheritance and Practical Use. Ph.D thesis, University of California, Davis.

Karim M A and Singh M P. 1984. Studies on fertility restoration in male sterile wheats derived from Aegilops-comosa cytoplasm. *Wheat Inf. Ser* **58**: 9-11.

Kaul M L H. 1988. Male sterility in higher plants. Monographs on Theoretical and AppliedGenetics 10. Springer-Verlag, Berlin.

Kihara H. 1951. Substitution of nucleus and its effects on genome manifestations. *Cytologia* **16**: 177-193

Kihara H. and Tsunewaki K. 1964. Some fundamental problems underlying the program for hybrid wheat breeding. *Seiken Ziho* **16**: 1-14.

Komaki MK and Tsunewaki K. 1981. Genetical studies on the difference of anther length among common wheat cultivars. *Euphytica* **30** : 45-53.

Kucera L. 1982. Monosomic analysis of fertility in common wheat. Prof. Marchal. *Euphytica* **31**: 895-900.

Kumar Shreekant and Ganguli D K. 1993. Heterosis and inbreeding depression in bread wheat. In. Heterosis breeding in crop plants. Theory and application : Short communications. Symposium, Ludhiana, 23-24Feb., 1993. [Edited by Verma M M, Virk D S and Chahal G S, Ludhiana, India, Crop Improvement Society of India, 62-63.

Larik A S, Mahar A R and Hafiz H M I. 1995. Heterosis and combining ability estimates in diallel crosses of six cultivars of spring wheat. *Wheat Inf. Ser* **80** : 12-19.

Leighty C E and Taylor J W. 1927. Studies in natural hybridization of wheat. *J. Amer. Soc. Agron* **10** : 865-887.

Leighty C E and Sando W J. 1924. The blooming of wheat flowers. *J. Agric. Res* **27**: 231-244.

Lelley J. 1966. Observation on the biology of fertilization with regard to seed production in hybrid wheat (In German) *Der Zuchter* **36**: 314-317

Liable CA. 1974. Chemical methods for pollen control. *Proc. 29th Ann. Corn and Sorghum Res. Conf. Pub* **29**: 174-182.

Liu B H and Yang L. 1994. Dwarfing sterile wheat and its use in breeding for dwarfness. *Scientia Agri. Sinica* **27(5)** : 17-21.

Liu Bing Hua, Wang Shan Hong and Li Yang. 1996. The discovery and identification of new material of nuclear male sterility in common wheat. *Hereditas* (Beijing) **18** (6): 9-11.

Ma Z Q, Zhao YH and Liu DJ. 1991. Incorporation of restoring gene of *Aegilops umbellulata* into wheat. *Genome* **34** (5) : 727-732.

Macer R C E. 1972. The resistance of cereals to yellow rust and its exploitation by plant breeding. Proceedings of the Royal Society, London B 181: 281-301.

Mahajan Vinay, Singh Kuldeep, and Kelkar R G. 1997. On the possibility of using CHA route in developing wheat hybrids. In. Abstract of Int. Group Meeting on Wheat Research Needs beyond 2000 AD. Karnal, pp. 41-42.

Mann S S. 1992. Genetic analysis for male fertility restoration in wheat. V. anomalous results of monosomics analysis. *Crop Sci.* **32**: 28-35.

Martin T J. 1990. Outcrossing in twelve hard red winter wheat cultivars. *Crop Sci.* **30** : 59-62.

McDaniel R G and Sarkissian I V. 1966. Heterosis: complementation by mitochondria. *Science* **152**: 1640-1642.

McIntosh R A and Cusick J E. 1987. Linkage map of hexaploid wheat. In: Heyne EG (ed). Wheat and wheat improvement-Agronomy Monograph No .13. 2nd edn, 289-297. Wisconsin, USA, ASA-CSSASSSA

Miller J F and Lucken K A. 1976. Hybrid wheat seed production methods for North Dakota. *Crop Sci* **16**: 217-221.

Molnar- Lang, Barnabas M B and Rajki E.1980. Changes in the shape, volume weight and the tissue structure of the pistil in the flowers of male sterile wheats during flowering. *Cereals Res. Comm.* **8**: 371-379

Murai K and Tsunewaki K. 1995. Photoperiod-sensitive Cytoplasmic male sterility induced in Japanese wheat cultivars by transferring *Aegilops crassa* cytoplasm. *Breeding Science* **45**: 199-203

Murai K, Ogihara Y and Tsunewaki K.1995. An EMS-induced wheat mutant restoring fertility against photoperiod-sensitive cytoplasmic male sterility. *Plant Breed* **114** (3): 205-209.

Nettevich E D and Naumov A A. 1970. The genetic characteristics of fertility restoration in wheat forms with cytoplasmic male sterility. *Nauch. tr. N IIs. kh. tsentr. r-nov nechernozemn-zony* **25** : 77-85.

Newton K J. 1988. Plant mitochondrial genomes: organisation, expression and variation. *Annual Review of Plant Physiology and Plant Molecular Biology* **39**: 503-532.

OECD. 1991. OECD scheme for the varietal certification of cereal seed moving in international trade. Organization for economic Co-operation and development, Paris.

Oehler E and Ingold M. 1966. New cases of male sterility and new restorer source in *T. aestivum*. *Wheat Inf Serv* (Kyoto) **22**: 1-3

Panayotov I, Gotsova D K and Gotsov K. 1986. Male fertility restoration against alien cytoplasm. I. comparison between the restoration abilities of three groups of lines. *Wheat Inf. Ser* **63**: 7-10.

Percival J. 1921. The wheat plant - A monograph. Duchworth & Co. London, pp. 463.Freeman, G.F. (1919). Heredity of quantitative characters in wheat. *Genetics* **4**:1-9.

Pickett A A. 1993. Hybrid wheat: results and problems. Adv. Plant Breed. *Suppl. J. Plant Breed* **15**: 1-259.

Picket A A, and Galway N W. 1997. A further evaluation of hybrid wheat. *Plant Cultivars and Seeds* **10**:15-32.

Qian C M, Xu A and Uiang G H. 1986. Effects of low temperatures and genotypes on pollen development in wheat. *Crop Science* **26**: 43-46.

Ralko V P. 1982. Effect of the maternal genotype on degree of pollen ferility restoration in wheat hybrids bred using male sterility. Vestsi AN BSSR, Ser Biyal.n. No 3, 33-38.

Rerkasem B and Jamjod S. 1997. Boron deficiency induced ear sterility in wheat (*T. aestivum L.*) and its implication for plant breeding. *Euphytica* **96**: 257-262.

Rodriguez R, Quinones M A, Borlaug N E and Narvaez I. 1967. Hybrid wheats: their development and food potential. Research Bulletin 3. International Maize and Wheat Im¬prpvement Center, Londres, Mexico.

Sage GCM. 1976. Nucleo-cytoplasmic relationships in wheat. *Advances in Agronomy* **28**: 267-300.

Schmidt J W, Johnson V A and Maan S S. 1962. Hybrid wheat. *Nebraska Experimental Station Quarterly* **9**: 9.

Singh S, Dhari R and Joshi A K. 1997. Expression of heterosis for yield and yield traits in Indian wheat crosses under drill sown condition, CIMMYT 1997. Book of Abstracts. The Genetics and Exploitation of Heterosis in Crops; An International Symposium, Mexico, D.F., Mexico. pp. 336-337.

Singh S K. 2003. Cluster analysis for heterosis in wheat [*Triticum aestivum* (L.) em Thell.]. *Indian J. Genet* **63** (3): 249-250.

Singh S K. 2005. Character association and path coefficient analysis for yield and floral characters in wheat (*Triticum aestivum* L. em Thell). *Crop Improv* **32** (2): 124-129

Singh S K. 2006. Evaluation of spring wheat [*Triticum aestivum* (L.) em Thell] germplasm for various floral characteristics. *SAARC. Jn. of Agri* **4**:167-177.

Singh S K and Joshi A K. 2003. Variability and character association for various floral characters in wheat [*Triticum aestivum* (L.) em Thell.]. *Indian J. Genet* **63** (2): 153-154.

Singh S K, Joshi A K and Arun B. 2007. Comparative evaluation of exotic and adapted germplasm of spring wheat for floral characteristics in the Indo-Ganetic Plains of India. *Plant Breeding* **126**: 559-564.

Singh S K and Singh R M. 2001. Variability and Character Association among Floral traits and Yield in Bread wheat [*Triticum aestivum* (L.) em Thell]. Indian J. Plant Genet. *Resour* **14** (2): 199-201.

Singh S K and Singh R M. 2004. Floral Biology and Character Association Studies in Wheat. *Farm Sci. J* **13**(1): 21-23.

Singh S K and Singh R M. 2006. Determination of optimum row ratio for hybrid seed production in wheat. *Annual Wheat Newsletter* **52**: 56-57.

Singh S K, Singh R M, Joshi A K and Dhari R. 2006. Effect of etherel on seed setting, outcrossing, pollen sterility and yield traits in wheat (*Triticum aestivum* (L.) Em Thell]. *Annual Wheat Newsletter* **52**: 51-56.

Sneep J, Murty B R and Utz HF.1979. Current breeding methods. In: Plant Breeding Perspectives. Eds: Sneep J, Hendriksen AT and Holbek O. Pub.: Centre for Agricultural Publishing and Documentation, Wageningen. pp 104-233.

Stehno Z. and Apltaverova M. 1980. Pollen sterility induced in wheat (*Triticum aetivum* L.) by the cytoplasm of *Aegilops* sp. *Sci. Agri. Bohenoslovaca* **12** (4): 245-253.

Stehno Z and Apltaverova M. 1981. The effect of the cytoplasm of alloplasmic lines of wheat (*Triticum aestivum*). *Sci. Agri. Bohemoslovaca* **13** (4):281-289.

Stroike J E. 1987. Technical and economic aspects of hybrid wheat seed production. In: Hybrid seed production of selected cereal, oil and vegetable crops, FAO Plant Protection and Production Paper 82, Food and Agriculture Organisation of the United Nations, Rome. pp 177-185.

Tsujimoto J and Tsunewaki K. 1984. Chromosome location of fertility - restoring gene of a common wheat Chinese spring for the Aegilops mutica cytoplasm. *Wheat Inf. Ser* **58**: 4-8.

Tsunewaki K, Endo T R, Kobayashi M, Mukai Y and Panayotov I. 1980. Genetic diversity of the cytoplasm in *Triticum* and *Aegilops*. Japan Society for the Promotion of Science, Tokyo.

Tsunewaki K. 1982. Monosomic analysis on the fertility restoration by *T. aestivum* cv. Chinese spring against *Aegilops ovata* cytoplasm. *Japanese J. Genet* **57** (5): 513-525.

USDA, 2007. Grain: World markets and trade. Dec, 2007. Pp. 7

Ushiyama T, Toriyama K, Tsunewaki K, Nonaka S, Shimada T and Nonaka S. 1996. Seed production ability of male sterile lines of common wheat induced by the interaction between an SV type cytoplasm and a 1BL 1RS chromosome. *Breed. Sci* **46** (3): 303-306.

Virmani S S and Edwards I B. 1983. Current status and future prospects for breeding hybrid rice and wheat. *Advances in Agronomy* **36**: 145-214.

Wang Yan, Liu Shu Ren, Zhai Yui Jie and Diao Yanling,1997. Studies on testing and utilization of heterosis in spring wheat hybrids. Acta Agri. *Boreali-sinica* **12** (1): 17-21.

Wilson J A. 1968. *Problems in hybrid wheat breading Euphytica* **14**, 1:13-33

Wilson J A. 1968b. Hybrid wheat developments with *Triticum timopheevi* Zhuk. derivatives. Proceedings of the Third International Wheat Genetics Symposium, Canberra 1968. pp 423-429.

Wilson J A. 1972. Hybrid Wheat Breeding. Rice breeding, Manila, Philippines, International Rice Research Station, pp. 593-602.

Wilson J A. 1984. Hybrid wheat breeding and commercial seed development. *Plant Breeding Reviews* **2**: 303-319.

Wilson J A and Ross W M. 1961. Cross breeding in wheat, Triticum aestivum. L Frequency of the pollen-restoring character in hybrid wheat having *Aegilops ovata* cytoplasm. *Crop Science* **1**: 191-193.

Wilson J A and Ross W M. 1962. Male sterility interaction of the *Triticum timopheevi* cytoplasm. *Wheat Inf Serv* (Kyoto) University **14**: 29-30

Wilson J A and Ross W M. 1962a. Cross breeding in wheat, *Triticum aestivum* L. II. Hybrid seed set on a cytoplasmic male-sterile winter wheat composite subjected to cross-pollination. *Crop Science* **2**: 415-417.

Wricke G. 1989. Genetic mechanisms for hybrid seed production. *Vortriige fur J1 lanzenzuchtung* **16**: 369-378.

Wrobel A. 1989. Genetic investigation of fertility restoration in male - sterile forms of wheat. *Hodowla Roslin Aklimatyzacja i Nasiennictwo* **29** (3-4): 13-26.

Zehr B E, Ratnalikar V P, Reddy L M M and Pandey LV. 1997. Strategies for utilizing heterosis in Wheat, Rice and Oilseed *Brassica* in India pp. 232-233 (Abstr B28)

In: The Genetics and Exploitation of heterosis in crops, 17-22 Aug 1997, Mexico City, Mexico.

Zeven A C. 1967. Transfer and inactivation of male sterility and sources of restorer genes in wheat. *Euphytica* **16:** 183-189.

Zhang G S and Yang T Z. 1989. A preliminary study on male-sterile lines of wheat with *Aegilops ventricosa*, *A. kotschyi* and *A. variabilis* cytoplasms. *Acta Agron. Sinica* **15** (1): 1-10.