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Perspective of hybrid wheat research: A review

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ABSTRACT

Hybrid technology in crop plants, especially cross-pollinated crops is successfully used for enhanced production. However, it remains unutilized in the self-pollinated crops, especially wheat. The future scope of hybrid technology in wheat depends on the male sterility systems, floral biology, level of heterosis and its exploitation of commercial level that may be useful in breaking yield barriers and enhancing the productivity in the major wheat belt of the country.

Key words: Crop, Heterosis, Hybrid technology, Floral biology, Male sterility system, Self-pollinated crop, Wheat

At global level, India ranks as second largest wheat-producing nation and contributes approximately 11.9% to the world wheat production from about 12% of global area (USDA 2010). China is the largest producer of wheat with 16.9% global wheat production. The other major wheat-producing countries are Russian Federation, United States of America and Canada and these 5 countries together contribute more than half of the global wheat production. The area under wheat throughout the world as well as in India has become nearly constant around 217.9 million ha and 26.9 million ha, respectively. The enhanced genetic potential of new genotypes by introducing the semi-dwarf, photoperiod-insensitive and fertilizer-responsive varieties and increased area under its cultivation during Green revolution era resulted in the increased productivity as well as production in India nearly 1% per annum. After Green revolution, although the improved pureline varieties kept on increasing wheat yields in the country but the average production level is hovering around 72 million tonnes during last decade with average productivity of 2.7 tonnes /ha. As per present population growth rate the population of India are expected to be around 1.3 billion by 2025 AD. Assuming 20% more per capita requirement of foodgrains, due to better standard of living and increase in the demand of processing industries, required wheat production will be around 109 million tonnes by 2025 AD (DWR 2007) . The north-western plains of the country comprising Punjab, Haryana, western Uttar Pradesh, plains of Jammu and Uttarakhand and northern Rajasthan 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 India has reached a sort of saturation level. To keep the productivity growth rate of 2.1% per year in order to meet out the projected demand of 109 million tonnes by 2025 AD, there is need to explore new innovative approaches 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 that offer a significant means of overcoming food shortages because of yield heterosis (Singh *et al*. 2004). However, Edwards (2001) explored the factors limiting the growth of hybrid wheat production and seed sales as insufficient levels of heterosis in a number of environments to justify the added hybrid seed costs, a low seed multiplication rate compared with other hybrid crops, and the complexity of the major hybridization systems.

The floral biology of wheat ensures that it is a 100% self-pollinated crop with occasional outcrossing of usually less than 1%. Although the heterosis was reported in wheat in early periods of 20th century (Table 1), the discovery of an effective cytoplasmic male sterility and pollen fertility restoration systems in wheat (Kihara 1951) opened up new avenues for commercial hybrid seed production. It is noteworthy that work on hybrid wheat has been carried out in the majority of countries having significant cropping areas under this cereal. Hybrid wheat is produced on a commercial basis in the USA, France, Australia and South Africa (Edwards 2001) and several countries, such as the China, India, USSR, UK, Denmark, Belgium, Germany, Bulgaria, Canada, Hungary, Italy, Japan, Mexico, Netherlands, Pakistan

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Table 1 A chronology of events related to hybrid wheat development

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)
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
1971 : DeVries commences publishing papers dealing with the suitability of wheat for cross-fertilization
1972 : ‘XYZ’ system proposed for the utilization of NMS (Driscoll)
1974 : First commercial CMS hybrid wheat released in USA
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
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
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
2003 : DWR and NCL Pune got US Patent (US2003/0192070A1) for chemical composition for complete male sterility, its process for preparation and use
2007 : ICAR (DWR) discontinued work on Hybrid wheat through CHA approach
2009 : ICAR initiated network project on Hybrid wheat using CMS approach

and Yugoslavia have active research and development programmes on hybrid wheat. Hybrid wheat has always been attractive to these countries that together produce more than 80% of global 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. Keeping all these facts in view, the research attempts were reviewed to make understanding about future strategic planning for hybrid wheat development.

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 6 possible factors to heterosis in wheat. It is possible for heterosis to be expressed by an F_1 hybrid in any part of the plant into which the products of photosynthesis are channeled. In this respect, it is necessary to consider the hybrid plant as a ‘source’ and ‘sink’ of assimilates. Virmani and Edwards (1983) have drawn attention to the need to balance these plant functions. Heterosis is unlikely to be directed exclusively towards factors associated with grain yield.

Commercial feasibility of a hybrid depend on 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, Singh and Kandola 1969, Singh and Singh 1971, Oury *et al*. 1990, Uddin *et al*. 1992, Borghi and Perenzin 1994, Singh 2003a) but most of them are based on space planted and small plots. The reports indicated that the hybrids developed through cytoplasmic male sterile (CMS) system resulted in less favourable yield advantage than the hand produced hybrids in field testing at optimum population rates (Allan 1973).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. Pickett and Galwey (1997) reviewed the development of hybrids of wheat and 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. The level of heterosis for grain yield ranges around 5–10% over purelines (Perenzin *et al*. 1998, Koemel *et al*. 2004, Kindred and Gooding 2005). However, significant standard heterosis of more than 20% was observed for yield and yield traits under drill-sown conditions (Singh *et al*. 1997, Zehr *et al*. 1997, Singh 2003b).

Yield components

Assuming that significant differences do not exist between hybrids and the line varieties in plant establishment or resulting population levels, heterosis in grain yield must, of necessity, arise from an increase in the production of one or more of the plant's yield components. The weight of grain produced from a single plant is the product of the number of fertile tillers/plant, grains/ ear and the weight of an individual grain. One of the principal underlying differences between the tillers and the number and weight of grain is the period of growth at which they are formed. As has been described by a number of workers including Sylvester-Bradley and Scott (1990), the establishment of potential tillers begins at the 4-leaf stage. Tiller fertility then is determined at different times later on (Evans *et al*. 1972, Kirby and Appleyard 1987) although the effect on grain number is to be decided early in floral development (Yu *et aI*. 1988). On the other hand, grain weight is largely determined in post-anthesis stage. Grains/ ear is of course the product of number of spikelets/ear and grains/spikelet. As already mentioned, many studies on hybrid wheat were undertaken on spaced plants. There has been a lack of correlation with the yield of normal density plantings. It is likely that yield components contributed in differing degrees to the lack of agreement between spaced plantings and normal cropping.

The expression of any potential heterosis for a component is likely to be strongly influenced by the environmental factors which may affect genotypes differently. However, many researchers have attempted to determine the component of yield responsible for heterosis in hybrid wheat. The principal studies of the source of grain heterosis indicated the tillers, grain number and grain weight as major components for realizing high yield potential. The results indicate that a single component is not the sole source of heterosis. This is not surprising since it is well known that there is considerable variation between line varieties of wheat in the performance of individual components. The inheritance of each of the 3 components of yield is highly complex with the involvement of many genes which may show different modes of inheritance and the negative compensation between components (Hsu and Walton 1970, Pinthus and Millet 1978). It has also been found that poor seed set may be associated with low levels of assimilate. The postulated benefits for hybrids have been considered from theoretical principles of the nature of heterosis and the mode of inheritance of the important genes. The findings supported the belief that heterosis arises as a result of the bringing together of dispersed dominant genes and non-allelic interaction. The question is complicated by additive genes and the fact that many characters are polygenically controlled, making the behaviour of the F_I difficult to predict for many characters. The contention that heterozygosity *per se* imparts increased vigour has very scarce experimental evidence. Moreover, the analogous belief of heterosis at the mitochondrial level in wheat has not been confirmed by investigations or by advances in molecular genetics.

Parental diversification for yield components: As the grain yield from a single plant is considered to be the product of the number of fertile tillers/plant, the number of grains/ear and the weight of an individual grain, there is need to have parental lines with better yield components that can be accumulated for harnessing heterosis at commercial level. Such parental lines can be developed by pre-breeding activities or diversification through utilization of diverse germplasm lines. Hermsen (1965) suggested pre-breeding as an integrated breeding approach in potato for the use of quantitative traits in distant species and defined it as a process in which the traits scattered in different accessions of a species are combined at one source. In order to widen the genetic base of bread wheat, the emphasis has been laid on introgressing genes from unexploited *buitre* types, synthetic hexaploids and Chinese sub-compactoid ear germplasm. The *buitre* lines has robust stem, long spikes, more spikelets, more grains/spike, large leaf area and broad leaves (Rodriguez *et al.* 1967). The synthetic hexaploids developed at CIMMYT were endowed with genetic richness for high grain weight, delayed senescence (stay green), high molecular weight (HMW) glutenins, resistance to Karnal bunt and yellow rust. Similarly, Chinese germplasm lines have robust stem, more grains/spike and new sources of yellow rust resistance. However, these elite germplasm had certain inherent limitations such as susceptibility to rust diseases and seed shriveling in *buitre* types, hard threshing, red grain colour, delayed heading and maturity in synthetic hexaploids and very soft grains (prone to insect damage) in Chinese material. These unique germplasms were evaluated for possible utility in hybrid programme as diverse gene pools and promising lines were used in breeding programme. The desirable attributes from *buitre* types, synthetic hexaploids and Chinese germplasm were introgressed into 'PBW 343' and 'WH 542' background. The advanced bulks developed through utilization of diverse matreial have shown wide range of variability. The introgression for 1000-grain weight (HT lines) was also observed from the Chinese Germplasm lines and a number of transgressive segregants were obtained having 1000-grain weight of more than 65 g. These lines also showed wide range for various yield component traits (Singh 2007).

FLORAL BIOLOGY

Floral structure, anthesis and anther dehiscence patterns in wheat make this crop strictly autogamous (Percival 1921, De Vries 1971). 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. The extent of natural outcrossing in cultivated varieties of wheat was observed up to 6.05% (Martin 1990, Hucl 1996, Singh 2006) which has positive correlation with length of flowering period. 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, Singh 2005), whereas anther length has been was observed from 3.0 to 5.09 mm (Kherde *et al.* 1967, De Vries 1974, Komaki and Tsunewaki 1981). Anther extrusion has been observed from 14.1 to 93.0% (Joppa *et al.* 1968, Singh and Joshi 2003). Phenotypic differences among wheat cultivars for days to heading, anthesis, anther size, pollen grain size, pollen viability, duration of floral opening and openness of florets were also observed (Chowdhary *et al.* 1994, Singh *et al.* 2007) and it was 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 to 98.6% (Hucl 1996, Singh and Singh 2001). In general, flowers of wheat reach their peak opening between 9 and 11.30 AM on a sunny day and subsequently, a second flush of flower opening occurs between 3 and 5 PM (Virmani and Edwards 1983). The largest separation angle between the glumes of first two florets of spikelet was found to be 16–40° and the wheat florets get closed within 12–20 min. of flower opening with extreme values being 11 and 66 min. (Percival 1921, Leighty and Sando 1924, Singh and Singh 2004). The effect of morphological traits such as spike laxness and lemma flatness on degree of floret opening in wheat was studied by De Vries (1971). 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 hr after the first round and florets remain opened for another 5 days (Molnar-Lang *et al.* 1980). Furthermore, within wheat cultivars, a large variation is reported for the number of pollen grains produced per anther. Under optimal field conditions (20^0C, 60% RH), wheat pollen is viable for approximately half-an-hour (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). Stigmas are receptive for 2 to 13 days after anthesis, and are most receptive for the first 2 to 5 days (De Vries 1971). Wheat pollen is relatively heavy compared with other grasses pollen and travels 1m from the pollen source (Lelley 1966).

The reports on correlation between floral traits are very meager. There is a positive association between anther size and the quantity of pollen produced /anther (Beri and Anand 1971). Anther length was reported to have positive correlation with number of pollen grains/anther (De Vries 1974) and flowering date (Komaki and Tsunewaki 1981). A close association between percentage of seed set in male sterile line and extent of synchrony in the heading of maternal and pollen parents was also reported (Araki 1990). Martin (1990) observed that outcrossing was positively correlated with length of flowering period but not with flowering date and plant height. The low association between spike traits and outcrossing rate was studied by Hucl (1996) who suggested that no single morphological trait can be used for predicting cultivar's outcrossing rate. The significant association of anther length with stigma length and anther extrusion with duration of floral opening was observed and it was suggested that the selection for the traits that promote outcrossing may result in the genotypes with more open pollination ability and these may be utilized as parents to improve yielding ability through enhanced heterozygosity (Singh 2006).

MALE STERILITY SYSTEM IN WHEAT

Wheat is monoecious and therefore, a line designated as female must not be allowed to produce pollen capable of fertilization 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 2 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. On the other hand, there is no direct genetic involvement in chemical hybridization or hand emasculation. Three methods for obtaining male sterility have been proposed for wheat: these utilise, respectively, cytoplasmic and nuclear genes, nuclear genes, or chemicals but CMS and CHA approaches are widely used in wheat as pollination control system. There are now more than 70 different male sterile cytoplasm (Murai 2002, Zhang *et al*. 2001, Hattori *et al.* 2002).

Cytoplasmic genetic male sterility system

This system is commonly known as CMS system and involves 3 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/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 hybrids in self-pollinated crops.

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 (1962a) discovered another effective source of male sterility in *T. timopheevi /* Bison cross. 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 *T. dicoccoides* var. spontaneovillosum, *T.* z*hukovskii*, *Ae. aucherii*, *Ae. ventricosa* and *Ae. kotschyi* were considered as the good sources of cytoplasmic genetic male sterility. *T.timopheevi* was observed to be major source of male sterility in wheat by several workers (Apltaverova *et al*. 1981, Ushiyama *et al.* 1996) and is now most widely used cytoplasm in hybrid wheat production.

Fertility restoration system: T. timopheevii and its derivatives were also observed as potential source of fertility restoration system in wheat (Wilson 1972, Panayotov *et al*. 1986). Other sources of fertility restoration in wheat were '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).

Genetics of male sterility - fertility system: Two incomplete dominant genes with epistatic action were noted to control fertility-sterility system in wheat. 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 up to 2 genes, designated as *fms1* and *fms2* for male sterility. Single recessive gene was also found responsible for male sterility (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. Although all the 3 mode of inheritance (monogenic, digenic and polygenic) was observed for fertility restoration, 3 genes located on chromosome 1A, 6B and 7D of *T. timopheevii* were found responsible for complete (Wilson 1972). Chromosome 1B of Chinese Spring was also identified as carrier of fertility restoration gene (Tsujimoto and Tsunewaki 1984). El-Kadi *et al*. (1983) observed 2-3 major genes in R line for fertility restoration while 2 dominant (Gotsova *et al*. 1987) and 2 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 2 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.

Interspecific 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 the cytoplasmic genes of the related alloplasmic species (Du *et al*. 1991). 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 (Maan 1992a). More than 10 different *Rf* genes from *T. timopheevii, Secale*, spelt wheat, emmer and wild emmer etc. relative species have been discovered and used in breeding R-lines. 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. 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.

Effect of cytoplasms: Different sources of male sterility system carry their own negative effects on growth and productivity of wheat. The cytoplasm from *T. 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, ear sprouting, etc. (Maan 1992b, Chen and Zhang 1994).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 F_1s and F_2s and did not result in harmful maternal effects.

Breeding scheme for F_1 hybrids using CMS: The CMS system of hybrid seed production requires 3 lines to produce single cross hybrid, 2 to provide a female parent and 1 for the male (Wilson 1984). 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 and requires 5-10 backcrosses to produce it (Zeven 1967, Tsunewaki *et al.* 1980, Bingham and Lupton 1987). 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 F_1 hybrid. Restorer genes are incorporated into the male parent by means of crossing programme and 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 conventional seed production arrangements. The restorer locus or loci will be heterozygous in the F_I hybrid. The basic system for producing an F_I hybrid by means of CMS is through crossing of A line with R line.

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 (Moore 1950) 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. Attributes of an ideal CHA have been suggested as selective induction of only male sterility with no effect on female fertility, production of readily apparent male sterile lines, no phytotoxic effect on the treated parent, effective on all genotypes of a species in a wide range of environments, systemic activity or persistence to sterilize early and late tillers or plants in the field population, flexibility in time of application to overcome adverse weather effects and to permit treatment of many hectares, considerable dosage flexibility to permit a safety margin for application, achieve sterility with a single treatment, does not adversely affect F_1 seed quality, or F_1 seedling or plant vigour, effective on several genera, economical to synthesize and practical to apply and safe and non-toxic to the environment (Virmani and Edwards 1983, Pickett 1993).

More than 40 chemicals have been patented as potential CHAs world over out of which etherel (Law and Stoskopf 1973) and maleic hydrazide (Chopra *et al.* 1960) are most commonly used. Complete male sterility by spraying of etherel was observed along with reduction in plant height due to reduced internode length, plant development, yield and increased number of fertile tillers (Rathgeb *et al.* 1982). Zhao *et al*. (1993) sprayed wheat crop with EK or ES (main component ethaphon) at 2 000–10 000 ppm concentration and obtained maximum male sterility at 6000 ppm ES and 7000 ppm EK. The female sterility and plant damage by maleic hydrazide was also observed (Porter and Weise 1961). A comparative study was made to study the effect of etherel and Maleic hydrazide (MH) and it was observed that the etherel was more effective towards reduction in seed set than maleic hydrazide (Singh *et al.* 1998). Other chemicals found effective in inducing pollen sterility are, KMS 1 (Zhao and Huang 1983), WL 84811 (Huang *et al*. 1988), LY 195259 (Tschabold *et al.* 1988) and CH 9701 (Mahajan *et al*. 1997). The shell compound WL 84811 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 reported at spike length of 7-8 mm (Mahajan *et al.* 1997), early stem extension stage (Savchenko *et al.* 1989), and early boot stage (Singh *et al.* 2006). Further, the late-sown crop was found more responsive to CHA than normal-sown crop (Singh *et al*. 2006). 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.

Genetic male sterility

A number of studies have been conducted for utilization of cytoplasmic male sterility system for hybrid production in wheat but some practical difficulties were proved in hybrid wheat breeding programmes using T-type cytoplasm induced male sterility. Firstly, the level of hybrid vigour was affected by the alien *T. timopheevii* Zhuk. Cytoplasm and secondly, the restoration of male sterility in the F_1 was genetically complex, incomplete and affected by genetic background (Kaul 1988, Rao *et al.* 1990). A new pollination control system for producing hybrid wheat seeds by the interaction between a genetic male sterility (GMS) gene and an added alien chromosome from a related species was proposed (Trupp 1971). A number of genes have been identified which prevent the production of pollen capable of fertilization. Genes controlling nuclear male sterility fall into 2 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 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. Usually recessive genes for male sterility are highly desirable because they usually facilitate identification of homozygous sterile progenies for F_1 production.

There have been many reports of genetic male sterilty (GMS) in wheat but only 5 GMS loci, 2 recessive (*ms1* and *ms5*) and 3 dominant (*Ms2, Ms3* and *Ms4*) have been located in wheat chromosomes so far. *ms1* and *ms5*, the recessive genes located to chromosome arm 4BS (Endo *et al.* 1991) and 3AL respectively. The locus *ms1* has 6 designated mutant alleles (*ms1a*, *ms1b*, *ms1c*, *ms1d*, *ms1e* and *ms1f*), whereas locus *ms5* has 1 mutant allele. The 6 *ms1* mutants were named Pugsley's – *ms1a* (Suneson 1962), Probus – *ms1b* (Fossati and Ingold 1970), Cornerstone - *ms1c* (Driscoll 1977); FS2 - *ms1d*, FS3 - *ms1e* and FS24 - *ms1f* (Sasakuma *et al*. 1978, Klindworth *et al*. 2002). The *ms5* mutant occurs in the wheat line 'FS 20' (Sasakuma *et al.*1978, Klindworth *et al*. 2002). Two of these mutants were produced by ionizing radiation (cornerstone and probus) and are presumed to result from terminal deletions of chromosome arm 4BS. However, Pugsley's mutant was a spontaneous mutant identified in an F_3 progeny of a cross 'Kenya farmer'/'Bearded Javelin 48' by Pugsley and Oram (1959) in Australia and likely to have an intact 4BS arm. Male sterility was transferred from this line to 'Chancellor' by Briggle (1970) has compatible genetic background for mst expression governed by this gene. The other 4 mutants, FS2, FS 3, FS 20 and FS 24 were chemically (EMS) induced (Franckowiak *et al.* 1976) and are therefore, likely have intact 4BS arm. Three dominant male sterile genes *Ms2*, *Ms3* and *Ms4* were located to chromosome arm 4DS, 5AS and 4DS respectively (Deng and Gao 1980, Bing-Hua and Jing-Yang 1986, Maan *et al*. 1987, Maan and Kianian 2001).

Systems of genetic male sterility in wheat: The obstacle to the use of NMS systems is maintenance of the male sterile parent. Normally, this is achieved within a heterozygous population (Hermsen 1965) but this conflict with the requirement that the female parent must not segregate for fertility in the hybrid seed production field. In principle, this applies for all species in which male sterile seed is produced by GMS; the problem is particularly serious for wheat because low multiplication rates make hand roguing of fertile segregants uneconomic and unsatisfactory. Maintenance requirements have, therefore, been the main consideration in the proposed systems for NMS production in wheat.

The 'XYZ' system: This system was designed to allow maintenance of a GMS line in which none of the 42 normal chromosomes carried a factor for fertility. Fertility to produce the female parent seed would be obtained from another line: identical except that it carried a chromosome addition encoding fertility. The XYZ system of producing hybrid wheat (Driscoll 1972, 1985) relies on the addition of chromosome 5R derived from *Secale cereale* L. to the male-sterile Cornerstone mutant (Driscoll 1977). The necessary fertility for maintaining the line would come from a corresponding fertility factor on a homoeologous alien chromosome addition line. A requirement of the XYZ system is that the alien chromosome should not pair with any from the normal com-plement. Since the dominant marker character—hairy peduncle associated with 5R—is an adult plant trait, differentiating between male sterile plants without the marker and the male fertile plants having the marker trait will take place at a post heading plant developmental stage in the field. So it is not a practical system, as it is difficult to rogue out the male fertile plants in the short time between heading and pollen shedding. A more efficient marker character associated with an alien chromosome is needed for logically modifying the XYZ system.

The 'VE' system: The line 'VE' was obtained from a cross of *T.vulgare* and *Elytrigia elongata,* the designation 'VE' being derived from the first letters of the specific names of the parents. When the line was grown in populations heterozygous for the dominantly controlled male sterility, the progeny is approximately 75% sterile (Shaowen and Shan 1980). This is used for bulk maintenance of the line. When male sterile seed is required, the segregants having normal fertility are first rogued from the population. The remaining plants, although largely sterile, produce enough pollen to allow selfing (Driscoll 1986). However, as a consequence of incomplete male sterility in the female parent seed, it is likely that the genetic purity of the hybrid produced will be rather low.

Other genes conferring male sterility

S 738: Athwal *et al*. (1967) reported a specific type of male sterility caused by the interaction of 3 recessive genes having an additive effect occurred in F_2 population of a composite cross received from Mexico. The degree of male sterility depends upon ms gene number: the lesser the number, the lesser is the expression of male sterility. Thus, the genotypes having 1, 2, 3 *ms* genes exhibit 36–49, 47–68 and 73–97% male sterility, respectively. This expression was further influenced by environment and by modifying genes.

UC 9109-9: It was identified in the progeny of dwarf × normal height cross in the USA and thought to be of mutant origin (Jan and Qualset 1977). Three recessive genes controlled this source. It resulted in a range of expression of male sterility which varied from very low levels of seed set when selfed to the transformation of anthers to pistil-like structures.

LZ mutant: A new wheat GMS mutant LZ was discovered in Lanzhou in Gansu province of China (Zhou *et al*. 2006). They successfully utilized the genetic male sterile mutant LZ in the 4E-ms system of hybrid wheat production and concluded that the mutant LZ has common wheat cytoplasm and carries a stably inherited monogenic recessive gene named *ms1g.*

Advantages and disadvantages of genetic male sterility: Wilson (1984) noted that despite very full investigations, GMS had not been utilized commercially for cereal crops. 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. 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 for this purpose, making it possible to select male hybrid parents from a wide range of varieties. In addition, GMS may also be used in recurrent selection schemes (Rao *et al.* 1990). 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.

Environment sensitive male sterility

The photoperiod, temperature sensitivity and nutrient deficiencies are also inducing the male sterility under some specific conditions. Photoperiod-sensitive cytoplasmic male sterility (PCMS) caused by an interaction between *Aegilops crassa* cytoplasm and *T. aestivum* cv. Norin 26 nucleus was first reported by Murai and Tsunewaki (1993). Alloplasmic 'Norin 26' shows almost complete male sterility under long-day conditions of 15 hr or longer, but male fertility under short-day conditions of 14.5 hr or less. The PCMS is maintained and multiplied by self-pollination under short-day conditions and hybrid seeds can be produced throughout crossing of a PCMS line with a pollen parent under long-day conditions. In contrast to the CMS system, this system requires only a PCMS line and a pollen parent (restorer line). Two kinds of fertility restoration systems against the PCMS are known in which, one is involved with a multiple fertility-restoring (*Rf*) genes in wheat cultivar 'Norin 61' located on (at least) chromosomes 4A, 1D, 3D and 5D, whereas the other is controlled by a single dominant major Rf gene *rfd1*, located on the long arm of chromosome 7B in the wheat cultivar "Chinese spring with atleast 20 modifiers (Murai and Tsunewaki 1994).

Jan (1974) reported thermo-sensitivity in wheat for producing genic male sterility. Certain wheat varieties carry genes, which render male fertility sensitive to environmental conditions such as reduced temperature (Qian *et al*. 1986). In regions having consistent climates, it might be possible to utilize such effects for production of F_1 hybrid seed for use in crop production in different environment. A genic male sterility system was developed in China, especially in regard to a temperature-sensitive male sterility system (reviewed in Sun *et al.* 2001). This system is a 2-line system without a maintainer. Cytoplasmic-genic male sterility in wheat with *Ae.umbellulata* or *Secale cereale* cytoplasm was also found stable in autumn and unstable in spring when grown in the glasshouse (Maan 1973) indicating photo-thermo sensitivity.

Deficiencies of copper (Agarwala *et al.*1980), boron (Rerkasem and Jamjod 1997) and some other micronutrients are reported to induce male sterility in wheat. High phenotypic variation has been reported in sensitivity to the deficiency of these micronutrients. reported that pollen sterility induced by copper deficiency in barley and wheat was found related to tapetum dysfunctioning characterized by cell hypertrophy that inhibits grain production (Jewell *et al.* 1988, Azouaou and Souvre1993). Rerkasem and Jamjod (1997) suggested the boron method of hybridization in wheat, in which boron deficiency was used as a selective medium or fertility and male sterile female parents and fertile male parents were provided by genotypic variation in the response to low boron content. Maintenance of female parents can be done simply in soils with sufficient boron content, unlike genetic male sterility, which can be maintained only in heterozygous populations. The chances for successful development of the method, however, could be strengthened by a better understanding of the physiological, genetic, and molecular bases for genotypic variation in response to low boron content.

COMMERCIAL HYBRID SEED PRODUCTION

The most important requirements of cross-fertilization and hybrid seed production are openness of flowers at peak flowering period, stigma receptivity to accept the pollen from male, pollen release from anthers outside the flower by good anther extrusion, presence of slight wind to carry the heavy pollen from male to female plants and pollen viability till fertilization. Low seed multiplication rate and in-efficient cross-fertilization are the two main constraints to hybrid seed production in wheat. In the hybrid seed production field, it is necessary to maintain careful separation of male and female parents to check contamination of hybrid seed 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 female : male 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 / ha 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-fertilization on seed yield and the cost of hybrid seed were also reported. The yield of hybrid seed can be computed as under for knowing the commercial feasibility.

$$\text{Yield of hybrid seed } (F_1) = a\ (b/100)\ (c/100)$$

Where, a is normal yield of wheat (tonnes/ha), b is area of female parent (%) and c is seed set (%).

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 pureline 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. to develop a practical hybrid wheat production scheme in Northern Mexico, based on the GENESIS (CHA) technology and to identify spring hybrid bread wheat 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 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 2 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 addressed the hybrid wheat development through CMS and CHA approach in network mode. Through CMS approach, cytoplasmic male sterile lines were developed by using *T.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 10–15 mm of spike length at 50–60 days after germination in most of the genotypes (Mahajan *et al.* 1997). Over 1 500 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 afternoon was suggested for enhanced outcrossing. 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 0.4 ha / hr. Besides, a seed sowing drill was also fabricated for simultaneous sowing of male and female parents for hybrid seed production.

Bottlenecks in research: The insufficient levels of heterosis, low seed multiplication rate and complexity of the hybridization systems were explored as major limiting factors for hybrid wheat development. The self-pollinated nature of wheat with occasional outcrossing of usually less than 1% makes the 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 more crucial for successful development of hybrids. These traits need to be investigated properly to identify the parents that can be put under conversion to male sterility system and fertility restoration. The discovery of an effective cytoplasmic male sterility and pollen fertility restoration systems in wheat using *Aegilops caudata* cytoplasm opened up new avenues for commercial hybrid seed production but the stability of male sterility across the locations is another bottleneck in the direction of development of hybrids which restricts the hybrid lines to the location specificity. *T. timopheevii* seems to be the most suitable one for commercial production of hybrid seed. The inclusion of yield potential in the bread wheat is also an important issue. As wheat in natural polyploid (allohexaploid), the transfer of donor traits from related species takes in more negative traits than the positive components. This needs strengthening of the pre-breeding activities for improving parental lines. 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.

Impact of research: Based on the results and experiences in Indian hybrid programme, it was concluded that out of two pollination control systems (CHA & CMS), the cytoplasmic genetic male sterility system, though cumbersome, provides useful, economic (Wilson and Driscoll 1983) 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 of parental lines (Le Gouis *et al*. 2002, Kindred and Gooding 2005) and preliminary testing of these hybrids on multi-locations. The multi-locations and multi-year data revealed that only few hybrids performed well. The investigations on floral traits have enabled to identify the genotypes that have floral traits for enhanced outcrossing and these lines are now used for parental diversification in the form of CMS and restorer lines in network mode research programmes. The heterotic combinations have been identified and 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.

Future strategies of hybrid wheat research

For a successful breeding programme and commercially viable hybrid seed production, 3 components are considered as basic criteria. These are the customer satisfaction for all important traits in hybrids, the seed cost for customer and the seed producer. 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. On the other hand, 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, yield of the crop in the farmer's field, commercial value of the crop per unit of land area, seeding rate of the crop, seed yield in the seed production field, extra yield to be expected from heterosis, 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 compared to maize, for example means that the ratio of male rows to female rows must be relatively high, and seed yield /ha is reduced correspondingly. If a hybrid has only a small yield advantage over the best pureline 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 returns. Research is in progress in several organizations 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 programmes 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 4 major wheat zones, i e north-western plains, north-eastern plains, central and peninsular zones. 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, the future research strategy for hybrid wheat development programme should consider the issues of 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 and promotion of active interaction between public and private organizations. Keeping in view the above, a network programme on development of wheat hybrids has been initiated with the breeding centres in north-western plains and peninsular zone to address the high fertility conditions as well as dry areas.

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