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An overview of hybrid wheat production in South Africa and review of current worldwide wheat hybrid developments

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Introduction

Increasing requirements of grain for food and industrial processes will require between 840 and 1050 million tons per annum to satisfy this demand, while the current world production is approximately 600 million tons. An annual production enhancement of 1.6 up to 2.6% is essential, even if the acreage increases. From table 1 it is clear that the current increase in yield obtained, will not be enough to keep up with the predicted rising demand for wheat.

With this situation in mind, the biggest challenge for wheat scientists is to achieve an increase of more than a 2.5%, in annual production, to keep up with the increased demand for food for the rapidly growing world population. Wheat breeders around the world have gone to great lengths to achieve a significant improvement in wheat yield levels. Wheat is one of the best adapted crops internationally, and is grown on all the continents, but there is now real concern whether wheat production will be able to keep up with the demands of an ever growing human population (table 1). In order to address this issue, plant breeders are looking at radical new technologies, including the exploitation of heterosis, to

Table 1 ■ Yield progression percentage per annum (FAO).

	1961-1963 to 1991-1993	1991-1993 to 2001-2003	1997-2020
All cereals (world)	2.3	1.0	1.04
Wheat developed countries	2.3	0.5	0.68
Wheat other countries	3.4	1.2	1.15

further improve the crop. Apart from raising the yield potential under favourable growing conditions, an important option must be to address the low yielding environments which still limit optimal yield expression on a significant percentage of the acreage on which wheat is grown (Jordaan, 1999).

Cukadar *et al.* (1997) stated that in order to reach the above-mentioned goal, breeders need to exploit new technologies to produce hybrid wheat. With this in mind, the development of hybrid cultivars has been identified by the Wheat and Maize Improvement Centre (CIMMYT) as a promising tool in a multi-tiered strategy for breaking the wheat yield barrier (Reynolds *et al.*, 1996).

Maize and rice, the two other major world cereals have the advantage of being produced as genuine hybrid crops. Therefore, it has become imperative that wheat selection should move quickly to hybrid types, in order to be able to attract more funds and remain competitive world-wide. With newly developed technology currently available, the development of hybrid wheat must receive at least some attention in most wheat breeding programmes.

History of hybrid wheat production in South Africa

Research and development of hybrid wheat has a long history. All the major events up to 1990 have been thoroughly summarized by Pickett (1993). He described the events chronologically starting with a proposal for hybrid maize by G.H. Shull in 1908 and ends with Cargill ceasing the development of hybrid wheat in the United States during 1990, yet continuing with commercialization in Australia and Argentina. The 259 pages of literature, published by Pickett during 1993, is the most extensive publication on hybrid wheat to date and used by various authors on a frequent basis (Cisar and Cooper, 2002).

With the discovery of the hybrid wheat mechanism during the mid-1960s, many private companies and several public research programmes devoted extensive resources to the development of wheat hybrids (Carver *et al.*, 2001). In South Africa the situation was no different. Since 1980, 13 F1 hybrid or facultative bread wheat cultivars have been released for production in South Africa (table 2).

The first introgression of CMS (Cytoplasmic sterility) and restorer genes was done between 1960 and 1970. In 1970 Sensako started the first hybrid wheat breeding programme in South Africa and in 1980 a Research and Development agreement between Sensako and DeKalb was established. The introduced line viz. H108 was released in South Africa in 1982 as the first hybrid (SNK108). In the decade between 1980 and 1990 Sensako evaluated a Shell Chemical Hybridization Agent (CHA) obtained from Nickerson, an amount of hybrid material was obtained from HybriTech to be evaluated under South African conditions and towards the end of the decade Cargill released various hybrids for the local market viz., Carina, Caritha and Carrol under the Carnia brand. The first hybrid wheat with Russian Wheat Aphid resistance (RWA), known as SST 936, was released during 1993. From 1997 to 2000 a total of four hybrids were released (table 2), which in addition to RWA resistance, had improved processing quality as well as yellow rust resistance. (The first epidemic of yellow rust developed in 1995). Both Carnia and Sensako hybrid breeding programmes were amalgamated in 1999 as a result of their acquisition by Monsanto.

In South Africa 800 000-1200 000 ha of wheat is planted annually of which +/– 7 372 ha consists of hybrid wheat. This is in less than one percent of the total wheat production in South Africa (personal communication, Patrick Graham, Commercial Director Sensako Wheat Programme).

No commercial hybrid seed will be available during the 2010 production season. Currently Sensako's hybrid wheat programme is running at a low profile when compared to the other breeding programmes. The main reason for this decision is the high cost of goods required to produce the F1 hybrid seed. The reasons and possible solutions will be discussed later.

Within South Africa there is a large spectrum of planting dates for winter wheat and genotypes vary in maturity, resulting from differences in vernalisation requirements (true winter types) or to day-length sensitivity (intermediate type). Thus, under these conditions, varieties exhibiting a vernalisation requirement can only be crossed with varieties with a photoperiod response at planting dates where the vernalisation can be satisfied.

Table 2 ■ History of hybrid releases in South Africa from 1980 to 2006.

Cultivar	Year of release	Growth type	Photoperiodic sensitivity	Female	Male	Commercial success
SNK104	1982	Winter	Yes	Na	Na	Not commercial
SNK108	1982	Winter	Yes	Na	Na	Good
Caritha	1987	Winter	No	Na	Na	Good
Carrol	1987	Winter	No	Na	Na	Average
Carina	1988	Winter	No	Na	Na	Very Good
SST 936	1994	Winter	No	A936	R41	Good
SST 964	1997	Facultative	No			Not commercial
SST 966	1997	Winter	No	A966	R41	Good
SST 972	1997	Facultative	No	A972	R41	Very Good
SST 983	1998	Facultative	No	A972	R44	Very Good
SST 935	2003	Winter	No	A966	R2	Good
SST 946	2004	Winter	No	A966	R6	Very Good
SST 963	2006	Facultative	No			Not commercial

R41 = winter growth type
R44 = winter growth type
R2 = extreme winter growth type
R6 = extreme winter growth type
A972 = facultative to spring growth type
A966 = facultative to winter growth type
A936 = facultative to winter growth type

Principles needed for successful hybrid wheat breeding programme

While commercial breeders developed procedures, in order to achieve total homozygosity, they followed in the footsteps of animal breeders to characterize populations as breeding units and introduced biometrical models to develop appropriate breeding strategies. Different recurrent selection procedures were devised to incorporate both additive and non-additive gene action (Comstock *et al.*, 1949). Together with reciprocal recurrent procedures (Hallauer and Miranda, 1981) the emphasis was put on selection procedures and theory. These theories formed the basis of a highly successful breeding strategy exploiting hybrid vigor in corn improvement. During the 1990s the interest of wheat breeders was once again focused on developing hybrids. Even those who claimed breeding to be more of an art, than a science, were making an effort to develop hybrid cultivars. Hollamby and Bayraktar (1996) also suggested that wheat breeders must again focus on producing hybrids, giving priority to procedures which were successful, especially in the development of hybrid corn.

This required a total change in the mindset of the wheat breeder, switching to a role model which was described by Sprague and Eberhart (1976):

1. Create two diverse breeding populations with maximum interpopulation cross performance.

2. Devise an effective selection programme to improve populations *per se*.

3. Identify hybrids with every cycle of selection.

Dreisigacker *et al.* (2005) proved that hybrid wheat, as a crop, has the potential to enhance yield performance and stability across diverse environments. Lang (1989) also identified three crucial pre-requisites for the successful implementation of hybrid wheat, viz. (i) a cost-effective system for seed production, (ii) adequate levels of heterosis, and (iii) the development of heterotic groups and patterns to ensure future progress through hybrid breeding.

Sterility systems

The production of commercial hybrid seed of wheat requires a system where a male sterile female parent is cross-pollinated efficiently, under field conditions, by the male parent and the resulting hybrids are fully self fertile.

The hybridization system must have the following properties, viz.:

1. It must not have secondary effects limiting the hybrid performances.
2. The system must be simple to use in selection programmes and easy to introgress into parental lines in order not to slow down the genetic progress.
3. The female male sterility must be totally effective in the seed production.
4. The fertility restoration must be complete and stable across the various environments where the hybrid is cultivated.

5. The system must be as cost effective as possible in terms of license or utilization rights.

6. The system has to be universal, in order to be suitable for the widest cultivation zone.

Cytoplasmic sterility (CMS)

Hybridization was made possible through the discovery of a *cytoplasmic male sterility* system in wheat (Kihara, 1951 and Kihara, 1958). As in many other crops, it changed the natural self-fertilized habit of wheat into a breeding system of cross pollination which could then be commercialized. The first workable cytoplasmic male sterile, nuclear-restoration system was described by Wilson and Ross (1962), when they reported that *Triticum timopheevii* cytoplasm induced male sterility with mainly neutral effects on agronomic and quality characteristics. This breakthrough led to the formation of a number of research programmes which investigated alternative cytoplasmic sources of male sterility within common wheat and the existence of nuclear genes necessary to restore fertility to the F1 hybrid. Wilson and Ross (1962) produced male sterile hexaploid wheat by substituting wheat cytoplasm with *Triticum timpoheevi* cytoplasm resulting in cytoplasmic (CMS) induced male sterility. Cross-pollination was then able to be accomplished. Male fertile F1-hybrids were produced when a fertility restorer genetic-factor was discovered by Schmidt *et al.* (1962). Virmani and Edwards (1983) described a total of 15 different cytoplasms in the genera *Triticum* and *Aegilops* that could form the basis for CMS systems. However, they also recognised that the *T. timopheevii* system had gained widespread use due to deleterious effects of the other available cytoplasms on various traits and/or because no advantage existed over the *T. timopheevii* system.

He *et al.* (1998) reported that the Chinese national hybrid wheat network originally used *T. timopheevii* based CMS, but they also reported that *Ae. kotschyi* and *Ae. ventricosa* were also being utilized as CMS sources. They reported that three hybrids based on *T. timopheevii* and six hybrids based on *Ae. kotschyi* CMS showed a 15 percent advantage over commercial pure line cultivars. Chen and Xu (2000) released a thorough summary of work done in China on CMS systems.

In order to produce fully fertile F1 hybrids containing the *Triticum timopheevii* cytoplasm, male sterile A-lines are crossed with restorer (R-lines). B-lines which have *Triticum aestivum* cytoplasm and the A-line nuclear genes are used to produce seed of the A-lines. The R-lines have fertility restoring genes (*Rf*), which produce fertility in the F1 hybrids. Unfortunately, expression of the *Rf* genes are not effective in all A-line genotypes and is a major obstacle in developing parental lines needed to produce hybrid cultivars (Samad *et al.*, 1997). Previous studies, to analyze the genetic and cytogenetic composition of R-lines, have indicated that one of two major *Rf* genes, one or two minor *Rf* genes together with several positive and negative factors can modify the conditions for proper operation of the *T. timopheevii* sterility-fertility restoration system of wheat hybrids (Robertson and Curtis, 1967; Maan *et al.*, 1984 and Bahl and Maan, 1973).

As mentioned, the CMS system requires complete and stable male sterility and complete restoration of the fertility status of the F_1 hybrid in a number of environments. Although R-lines have been developed with complete fertility restoration properties, the main obstacle still remaining is to create significant genetic progress in developing agronomically improved R-lines. The use of marker-assisted selection for *Rf* genes, by means of restriction fragment length polymorphism (RFLP), appears to increase the probability of making agronomic progress while retaining *Rf* genes in the male population (Ma and Sorrells, 1995).

Today, among all the existing Cytoplasmic Male Sterility systems, CMS *timopheevii* appears to be the most reliable, even if currently only operational in the dryland territories of South Africa, India and Australia. It is, therefore, crucial to develop molecular markers for facilitating the reconversion of inbreds.

Nuclear male sterility

Taigu nuclear male-sterility was discovered in the Taigu County, Shanxi Province of China in 1972. It is controlled by a dominant gene, *ms2*, also historically called *Ta1* by Chinese scientists (He *et al.*, 2001). It has been widely used in recurrent selection and was also employed as a crossing tool within conventional breeding programmes.

Nuclear male sterility was discovered by Wilson and Driscoll in 1983, but failed because of the expensive methods of maintaining the seed stocks.

Chemical hybridization agents (CHA)

The most significant achievement in hybrid wheat seed production was the development of Chemical Hybridizing Agents (CHA) to sterilize male wheat plants. Chemical Hybridizing Agent (CHA) is the term that has gained the most widespread acceptance to describe the group of chemicals which contains the ability to affect male and/or female sterility (Cisar and Cooper, 2009). In a publication, by McRae (1985), he discusses the origin of the terms *gametocide* and *CHA* and suggests that the latter enters the scientific literature as a misnomer. He suggests that the term CHA is broad enough to embrace all modes of action and does not associate gametes with pollen. The first generation of chemical compounds that was tested as CHAs were developed for other purposes, such as anti-lodging or height-reducing agents. They generally caused a high degree of phytotoxicity at rates required to establish adequate sterility. This often resulted in poor female receptivity or fertility, or even failed to produce adequate male sterility over a range of environments (Cisar and Cooper, 2009). Although the first results were disappointing, it was reported that the chemicals R.H.007 and WL 84811 which were developed by the companies Rohm and Haas and Shell, respectively, were regarded as successful. The following researchers: Bruns and Peterson (1996) from the USA, He *et al.* (1997) from China and Perenzin *et al* (1997) from Italy, simultaneously, reported on the effective use of CHA products to produce hybrids.

The current generation of CHAs, was specifically developed for its male pollen-suppressing activities. Significant improvements have been achieved to reduce phytotoxic effects. Improved seed quality, on a wide array of genotypes, has also been observed. The Shell compound WL 84811 and the Monsanto CHA namely GENESIS are good examples of the latter group of chemicals. Development of WL 84811 has been discontinued, but GENESIS has received full commercial registration in the United States and a provisional registration in France. It is currently being used in commercial production of hybrid seed on both continents (Cisar and Cooper, 2009).

According to Carvis and Cooper (2009), CHA products should have distinct advantages over CMS. One major advantage is that the use of CHAs shortens the development period for hybrids, since female lines need not be developed by backcrossing (which normally has to be done by hand) and seed multiplications by using the female maintainer line as a pollen parent are avoided. This technology facilitates the implementation of recurrent selection procedures, and produces enough seed for trial purposes at an earlier generation to carry out extensive testing throughout the target area. Test crossed seed on CMS female lines can be produced from pollen of a male tester in an isolated crossing block. Females having normal cytoplasm can be test crossed in a three-way hybrid by hand crossing the females to the female component (A-line: sterile) of the female tester line and pollinating the resultant sterile F1s with the male tester line (restorer).

Carvis and Cooper (2009) summarized the advantages and disadvantages of CHA, expressed by various researchers in their studies, in order to develop hybrid wheat cultivars (Wilson, 1984 and Virmani and Edwards, 1983).

These advantages include:

1. Breeding procedures are simplified since this system does not require conversion and maintenance of the A-line, or the breeding of fertility restoration into male parents.
2. Genotypes with poor anther extrusion can still be used as female parents.
3. Evaluation of large numbers of lines, for general and specific combining ability and for seed production characteristics, is simplified.
4. Development and improvement of heterogeneously diverse breeding populations, such as Reid and Lancaster open-pollinated maize cultivars or the Kafir and Milo sorghums, are made possible.

These authors also discussed disadvantages of CHAs, including:

1. Reduced seedset of CHA females versus CMS females due to chemical overdose effects.
2. Difficulty of optimum field application of the CHA due to weather conditions.
3. Required evaluation of genotype x environment interactions, with the efficiency of the CHA system diminishing if many years or locations are required to determine optimum dosage rates.
4. Male fertility, or selfing, in hybrid production fields, which can result in seed lots that do not meet seed law standards for a hybrid;
5. Costs associated with identification, development and registration of the compound.

Hybrid seed quality produced under field conditions may be compromised if sterility of the female parent is not complete. Several methods for assessing the efficacy of the CHA treatment of the female parent exist but they display varying degrees of success. These methods include the use of bags or pollen tents to prevent external pollination, close monitoring of the production field and the use of electrophoretic or chemical tests (Carvis and Cooper, 2009).

The use of pollen bags or tents gives an objective assessment of sterility of a comparatively large population at a relatively low cost. Any seeds set under bagged heads is presumably the result of self-pollination, indicating that complete sterility levels were not achieved. It should be noted that bagging itself, might cause reduced seed sets, which must be accounted for in the assessment of sterility. It is often more practical to simply monitor the treated female plants and then observe the percentage of sterile and open florets a few days after the stigma has reached the receptive stage. Depending on the mode of action regarding the specific CHA being used, it may also be possible to observe the dehiscence of fertile pollen from the anthers, as is the case with GENESIS. Generally, complete flower opening will not occur if plants have a significant amount of self-fertile pollen (Carvis and Cooper, 2009).

When making use of a chemical hybridising agent (CHA) it is possible to make reciprocal testcrosses at will, while in the case of cytoplasmic male sterility genetic systems (CMS) testcrosses to a male tester line should be delayed to follow cytoplasm substitution backcrosses. The rate of producing hybrids between the two pools can be improved by enforcing homozygosity at an early stage of line development. Haploid breeding techniques will reduce generation time and increase genetic gain (Howes *et al.,* 1996). Sensako owns a very efficient haploid laboratory which assists the hybrid breeding programme in developing improved parent lines.

Genesis was tested during the 2004 season in the South African hybrid wheat programme. However, the results under South African conditions were not satisfactory enough to promote the CHA application to a commercial situation. Ammar *et al.* (2005) reported effective results with Genesis under well controlled conditions regarding the sterilization of a majority of lines used as female parents. However, the seed production levels were very low and varied from 0 to 35%. They observed that the major limiting factors were poor pollen production and lack of adequate anther extrusion in the lines used as males. They also tried to use localities with improved wind movement but without any satisfactory results.

Conditional genetic male sterility or two-line system

Shi observed in 1980 that some conventional rice varieties became fertile in long days accompanied by high temperatures, while in short days accompanied by cooler temperatures these varieties became male sterile. This opened the way to the development of a very productive two-line hybrid rice variety. Following the same concept, a few Chinese breeding teams are currently trying to develop a related system in wheat (Zhang *et al.*, 2001; Guo *et al.*, 2006 and Quan *et al.*, 2007), with the female being fertile in Beijing (40° North latitude), and the hybrid seed production taking place to the south of this location, around 33° North latitude. However, this system will be very difficult, or even impossible to implement in regions which do not have a large range of latitudes. The level of the resulting hybrid seed rate varies according to the prevailing annual weather patterns.

Genetic sterility with an additional chromosome

The concept on which this system has been based was created by the Weizman Institute in Israel. This recessive sterility is very stable and nearly all wheat lines can be used as male restorers. The bottleneck is maintenance of the female lines. In order to overcome this obstacle, interspecific crosses have been used and maintainer lines, with an extra chromosome have been created. Some Chinese teams have developed related systems, which are more or less efficient where the maintainer and female seed can be distinguished by different colors (Zhou *et al.*, 2006).

Comparison of main existing hybridization wheat systems

Table 3 ■ Comparison of main existing hybridization systems according to a score developed by Alain Bonjean (unpublished).

Hybridization systems	**Sterility stability**	**Restoration ease**	**Negative secondary effects**	**System universality**	**FTO**	**Female seed multiplication ease**	**Inbred introgression ease**	**System availability**	**Comments**
CMS *timopheevii*	+ –	– – +	+ –	– – –	+++	+ –	+ –	+ + +	Best CMS system
Gametocides	++–	+++	– – –	+	– – +	+++	+++	+–	License will probably not be renewed
2 line system	++ – –	++?	–?	– – –	– ++	++ –	– –	++ – –	Only works in some environments
Genetic system with extra chromosome	+++	+++	+++	+++	– ++	– –	+ –	– –	Not operational, needs improvement
GM system	+++	+++	+++	+++	++ –	+++	+++	– – –	Not operational, plus authorization to be obtained for release

+++ = highly favourable application possibilities (highest score).
+ = low favourable application possibilities.
– – – = huge amount of difficulties are experienced in application possibilities (highest score).
– = some amount of difficulty is experienced in application possibilities.

Heterosis

The term *heterosis* is synonymous with *hybrid vigour* and is the expression of the superiority of the F1 performance relative to the parental performance. It is, therefore, fundamentally concerned with inbreeding as well as out breeding (Goldman, 1997). It was not until a landmark paper by Shull during, 1908, that the fundamental principles of inbreeding and out breeding and their role in heterosis, had been clarified. Shull was, thus, responsible for naming the word *heterosis* during 1914.

Vigour exceeding the levels expressed by the parents is called *hybrid vigour* or *heterosis*. Hybrid vigour relies on the genetic dissimilarity of the gametes which fuse during fertilization (Mather, 1955). This phenomenon has been argued on statistical/quantitative grounds (Lamkey and Edwards, 1997), as well as on molecular grounds (Stuber, 1997), in order to understand the effect of over dominance, dominance and epistasis determining the genetic basis thereof. Although the exact genetic basis of heterosis has not been understood or determined yet, breeding methods were empirically developed to exploit the heterosis expressed (Hallauer, 1997). It is generally accepted that the utilization of the effect of heterosis is one of the greatest achievements in plant breeding of the 20th century.

According to Mayr (1997), quantitative genetics is the theory which links the phenotype to the genotype. Quantitative genetics, therefore, fulfils an important role in any plant breeding programme, because the phenotype represents the part which is visible to the plant breeder (Mayr, 1997). Selection has an indirect influence on the genotype, because the phenotype is a result of the observed interaction between the genotype and the environment. It can, therefore, be concluded that quantitative genetics also plays a fundamental role in the manipulation and exploitation of heterosis, because heterosis is a phenotypic phenomenon (Mayr, 1997).

Quantitative genetic theory suggests that high heterosis values can be expected in a hybrid if the source population has (i) a high frequency of genes with partial or complete dominance and/or (ii) maximum differences in gene frequencies of over dominant loci (Hallauer *et al.*, 1988). For optimal heterosis exploitation, parents should be derived from different genetic backgrounds or pools, commonly referred to as heterotic groups (Melchinger and Gumber, 1998).

During the last four decades, hybrid wheat research has mainly focused on the introduction of male sterility and on developing lines with acceptable cross-pollination characteristics (Pickett, 1993). However, knowledge about hybrid performance, the relative importance of general (GCA) and specific combining ability (SCA) and genetic background of the parental materials for maximum exploitation of heterosis in wheat, still remains limited. Therefore, Dreisigacker *et al.*, (2005) carried out a study to determine the latter and found that the level of heterosis, in spring wheat, was too low to warrant commercial exploitation of hybrids.

Melchinger (1997) stated that heterosis increases with genetic distance among the parents up to a certain optimum level of divergence and then decreases. A further important aspect, in this context, is the adaption of the parents to the target environments.

Genetic theories for heterosis are (i) dominance, including linked dominant favourable factors, (ii) true over-dominance and (iii) certain types of epistasis.

According to Duvick (1997a) heterosis had been responsible for much of the yield gains in crops such as maize, sorghum and sunflower, but the effect was indirect. The indirect benefits include: (i) Precise genotype identification and multiplication, instead of a random collection of hybrid/inbred plants in an open pollinated variety. The most superior hybrid combinations can be identified and reproduced at will in unlimited quantity. (ii) Breeders of hybrid crops can react faster and have more options available to meet changing times and changing demands. New hybrids with required traits can be made and tested within one or two seasons, given a broad-based pool of inbred lines. (iii) Farmers can easily identify hybrids in comparison to the open pollinated varieties. They normally expect more from hybrids and would, therefore, be more willing to apply extra inputs. (iv) The prospect of annual seed sales at profitable prices attracts private capital to hybrid breeding and sales.

There has always been some degree of free exchange of wheat germplasm amongst wheat breeders. The significance of this, together with the resulting availability of genetic diversity, cannot be underestimated and is regarded as one of the major reasons for the observed success of present day wheat breeding (Kronstad, 1996 (a) and Kronstad, 1996 (b)). Winter and spring wheat are regarded to be genetically diverse because of their adaptation to different ecological environments and historical isolation.

Kronstad (1996a) found that crosses between spring and winter wheat gene pools showed higher heterosis values than crosses within the gene pools. This created the opportunity for wheat breeders to develop hybrid wheat using the spring and winter germplasm as parental populations, as one of several options. However, breeders have used this genetic variability in a systematic way to improve spring as well as winter type backgrounds by intercrossing the two gene pools. The classical example is the Veery lines, where Kavkaz (representing the East European winter germplasm) was crossed to Buho"s" // Kalyansona/Blue Bird (representing the spring wheat gene pool). It was estimated by Kronstad, (1996a) that more than 5 million hectares was grown under those lines and that about 80 percent of the advanced spring wheat lines at CIMMYT carried winter wheat germplasm in their parentage, at that stage. Never the less, Cukadar *et al.,* 1997 proved that heterosis exists in CIMMYT wheat lines. The spring by winter crosses are only one example demonstrating the existence of heterotic patterns and there may be many more. Cox and Murphy, (1990) stated that the lack of knowledge regarding heterotic grouping of parental germplasm can be regarded as the major limitation of producing competitive hybrid cultivars.

Globally, wheat heterosis is mainly linked to biomass increase by virtue of:

1. Tall plants with the use of semi-dwarfing genes to avoid lodging.
2. 1000 kernel weight usually 10% superior to parental lines, which indicates a better performance of the hybrid to "fill" grains (Zhang *et al.*, 2001 and Gong *et al.*, 2006).
3. Denser and stronger root system.
4. Better tilling capacity (Bertan *et al.*, 2009) allowing a decrease in sowing density and the use of phyto-chemical products as it reduces the vegetation density.

5. Improved yield stability across various agro-environments (Burns and Peterson, 1998) linked to a better use of space and an improved tolerance to temperature stresses.

Heterosis for yield

Sun *et al.* (1997) claimed that hybrid wheat had the potential to provide not only increased yields but also stability across a range of environments. They stated that the level of heterosis remained the major limiting factor for the commercial use of hybrid wheat. On average only 8 to 10% heterosis over mid-parent values were observed in the F1 hybrids, while parental combination with over 20% heterosis were rare among the germplasm pool at that stage. The many similarities among parental lines were the most logical explanation for the previous statement. Therefore, they proposed that it was necessary to identify divergent heterotic groups which would improve the level of heterosis.

Urazaliev *et al.* (1997) reported heterosis levels for yield between 4 and 25% in soft wheat genotypes. Hybrid yield increases of 30% and more in comparison to their parents have been reported by Duvick (1997b). However, when new hybrids have to comply with certain minimum quality requirements, thus maintaining milling and baking quality, such crosses typically yield only 5-15% more than their parents. The highest heterosis for yield in a study carried out in India, was 24.48% for a specific hybrid cross combination (Singh *et al.*, 1997). They also stated that heterosis below 20% would be considered unacceptable in order to justify commercial usage of hybrid wheat cultivars.

Bedo *et al.* (2001) showed that the F1 performance of Hungarian hybrids was between 3 and 10% better than the average of the released varieties and up to 5% better than the average of the four best inbreds. According to Cisar and Cooper (2009), standard heterosis can be described as the comparison of a hybrid to a local check cultivar. The heterosis values for yield that, they had observed, ranged from 3.8 to 32.1%.

Ammar *et al.* (2005) reported best-parent heterosis values that varied between 0 and 31% and commercial heterosis (in comparison to the most widely used commercial check) varied between 0 and 25%. They also observed that a positive correlation exists between best-parent and commercial heterosis when all the hybrids, they tested, were taken into consideration, but that the results per male basis indicated that the males which produced the highest frequency of hybrids, with statistically significant best-parent heterosis, were generally those producing very few or no hybrids with statistically significant commercial heterosis and vice-versa. They concluded that hybrid yield was controlled, primarily by additive gene action, and thereby could be fixed in a pure breeding line.

In South Africa during the 2001 season a decision was taken to discontinue the production of the two facultative hybrids, viz. SST 972 and SST 983, due to economic reasons. In order to determine acceptable standard heterosis values for

Table 4 ■ Yield comparison regarding true winter growth type hybrids for the Free State region during the production seasons 2000 to 2003.

	2000		2001		2002		2003		Average	
Cultivar	**kg/ha**	**Dev(%)**	**kg/ha**	**Dev(%)**	**kg/ha**	**Dev(%)**	**kg/ha**	**Dev(%)**	**kg/ha**	**Dev(%)**
SST 936	2830.00	10.25	2759.00	13.35	2793.00	11.99	1933.00	1.26	2578.75	9.69
SST 966	2764.00	7.67	2734.00	12.33	2807.00	12.55	1838.00	– 3.72	2535.75	7.86
#	2567.00	0.00	2434.00	0.00	2494.00	0.00	1909.00	0.00	2351.00	0.00
LSD (p = 0.1)	146.33		106.66		193.33		121.00		141.83	

= Best commercial check.
Dev (%) = Deviation according to best commercial check.
Kg/ha = Average yield expressed in kilogram per hectare.
LSD = Least significant difference at 90% confidence level.

both the facultative as well as the winter growth type hybrid cultivars, only the yield data between the 2000 and 2003 production seasons were taken into consideration. When there is a large spectrum of planting dates available for winter and facultative wheat cultivars due to differences in vernalisation and photoperiod requirements, cultivars with similar characteristics regarding the above-mentioned growth periods are grouped together and evaluated in separated trials. The yield comparisons of these hybrids and the corresponding best commercial cultivar, included in the trials, are shown in table 4 and table 5.

Jordaan *et al.*, (1997) stated that the hybrids which expressed the highest level of heterosis were those proved to be daylight sensitive but with little or no vernalisation requirements. At present the best hybrids in this class (SST 972 and SST 983) are heterozygous for the (Vr) genes but are pure breeding for the day-length, sensitive genes (facultative/spring genotype).

From table 4 it is clear that the winter wheat hybrids, viz. SST 936 and SST966, produced significantly higher yields except for the 2003 production season. Standard heterosis levels varied from 1.26 to 10.25% in comparison to the best corresponding commercial check. The 2003 season was a year in which severe moisture stress conditions were observed during the kernel filling period and this drastically reduced the yield advantage of the hybrids over best commercial check.

Significant higher yield performances, except for the 2003 production season, were observed for both SST 972 and SST 983. Standard heterosis values between 0.19 and 21.74% were observed for both the facultative wheat hybrids (table 5). This strengthens the argument from Kronstad (1996a), that the best heterosis values are being obtained between two diverse heterotic groups. If one takes the international norm into consideration, which states that standard heterosis values must be higher than 20% to justify the development of hybrid wheat, then the latter two cultivars are a good example.

There are various statistics available to describe the yield stability of a genotype in a range of environments, with varying yield potential. Lin and Binns

Table 5 ■ Yield comparison regarding intermediate growth type hybrids for the Free State region during the production seasons 2000 to 2003.

	2000		2001		2002		2003		Average	
Cultivar	**kg/ha**	**Dev(%)**	**kg/ha**	**Dev(%)**	**kg/ha**	**Dev(%)**	**kg/ha**	**Dev(%)**	**kg/ha**	**Dev(%)**
SST 972	2905.00	8.23	2736.00	15.49	2751.00	21.08	2015.00	– 5.04	2601.75	10.16
SST 983	2847.00	6.07	2728.00	15.15	2766.00	21.74	2126.00	0.19	2616.75	10.80
#	2684.00	0.00	2369.00	0.00	2272.00	0.00	2122.00	0.00	2361.75	0.00
LSD (p = 0.1)	137.00		119.67		165.33		131.00		138.25	

= Best commercial check.
Dev (%) = Deviation according to best commercial check.
Kg/ha = Average yield expressed in kilogram per hectare.
LSD = Least significant difference at 90% confidence level.

(1988a and 1988b) proposed a stability concept uniquely different from other models. This concept is known as the *Cultivar Superiority Measurement* (P_i) and is defined as the P_i of genotype, *i* as the mean square of distance between genotype *i* and the genotype with the maximum response. The smaller the value of $P_{i,}$ the less its distance from the genotype with the maximum yield, and thus better the genotype. Although most plant breeders prefer to describe genotype by environment interaction as a linear response to environmental yield potential and the deviations from that response as originally proposed by Eberhart and Russel (1966), the Sensako breeding programmes normally use the Cultivar Superiority Measurement as an indication of yield stability.

The Cultivar Superiority Measurement values for both the winter and facultative growth type hybrids can be seen in table 6 and 7 respectively.

In table 6 it is evident that both the hybrids, SST 936 and SST 966, produced not only significantly higher but also more stable yields than the best commercial check. Similar results were obtained for the facultative hybrids. The C-values for the latter hybrids were even lower than that of the winter hybrids indicating that SST 972 and SST 983 produce higher and more stable yield over localities and years (table 7).

Table 6 ■ Cultivar Superiority Measurement (C-value) values for true winter growth type hybrids for the Free State region during the production seasons 2000 to 2003.

	2000	2001	2002	2003	Average
Cultivar	**C-value**	**C-value**	**C-value**	**C-value**	**C-value**
SST 936	111.00	63.00	90.00	74.00	84.50
SST 966	158.00	93.00	98.00	158.00	126.75
#	260.00	253.00	246.00	140.00	224.75

= Best commercial check.
C-value = Cultivar Superiority Measurement.

Table 7 ■ Cultivar Superiority Measurement (C-value) values for facultative growth type hybrids for the Free State region during the production seasons 2000 to 2003.

Cultivar	2000 C-value	2001 C-value	2002 C-value	2003 C-value	Average C-value
SST 972	70.00	26.00	11.60	142.00	62.40
SST 983	118.00	21.00	9.60	81.00	57.40
#	193.00	182.00	228.00	94.00	201.00

= Best commercial check.
C-value = Cultivar Superiority Measurement.

These results confirm the results reported by Sun *et al.* (1997) that hybrid wheat produces higher and more stable yields than traditional open pollinated cultivars. This was the main reason for the popularity of SST 972 and SST 983 amongst producers before they were discontinued.

Heterosis for quality traits

The Wheat Board (established in 1938) introduced wheat trade based upon quality criteria (Fowler and Priestley, 1991) and remained the sole purchaser of all wheat produced in South Africa until the deregulation of this single channel wheat marketing system in 1997. Since then, the decontrolled free trade environment has been established and the wheat industry as a whole (wheat breeders and the processing industries, in collaboration with the agricultural sector), is now responsible for the control and maintenance of the quality standards of grain for the different market sectors. Wheat marketing systems are constantly changing and the trend is towards identity-preservation and the so-called "*niche-market*" or "*closed-looped*" marketing systems in which special quality wheat is contracted at a premium price. Quality is, therefore, becoming more and more important to the wheat farmer, breeder and industry in South Africa. Local breeders mainly develop hard red bread wheat which has to meet certain requirements. It needs to comply with 19 quality characteristics (milling and baking) over a three year data period, as set by the industry. The millers are interested in the highest flour yield and ease of milling. Bakers, on the other hand, are interested in receiving a constant grade of grain, whereas farmers cultivate wheat to comply with three of these characteristics (test weight, protein content and falling number) when delivering their harvest to silos (personal communication, J.D. Cilliers, SENSAKO).

One of the reasons raised for the failure of hybrid wheat (Jordaan, 1996) was the erosion of genetic diversity caused by the introgression of unrelated germplasm in a background with acceptable adaptation, milling and baking characteristics.

A recent MSc. study conducted by Elaine van Eeden (awaiting publication), has been initiated to determine the quality characteristics of hybrid wheat in

South Africa, the influence of the male and female parents on quality and to assess heterosis in hybrid wheat quality. The stability performance of the hybrids, their parental lines and conventional cultivars were also determined. A further objective was to assess sprouting tolerance in hybrid wheat. Twelve hard red genotypes were planted at six locations throughout the Free State in separate winter (WHPT) and facultative trials (IHBPT), during 2004 and 2005. A separate sprouting and falling number trial consisting of 25 genotypes was planted at Bethlehem during 2004 and 2005 to evaluate the sprouting and falling number problem in hybrid wheat and included males, females, hybrids and conventional cultivars. Heads were cut at physiological maturity and thereafter with seven day intervals, for evaluation in a rain simulation facility.

Mean squares were highly significant for genotype, environment and year for test weight, SKCS kernel size, Hagberg Falling Number (HFN), ash content, alveograph strength and mixograph mixing time in both trials. Highly significant differences were observed in hardness index, break flour yield, flour yield, consistograph water absorption in the IHBPT trial and wet gluten content in the WHBPT trial. The males mainly contributed to poor quality, with the females and conventional cultivars having acceptable quality. The hybrids, from high quality parents, were generally of better quality. Positive heterosis was expressed for test weight, SKCS kernel size and mixing time and negative heterosis for HFN, ash and alveograph strength for both the intermediate and winter trials. Negative heterosis was revealed for the hardness index, flour yield and consistograph water absorption in the intermediate trial and wet gluten content in the winter trial. AMMI stability values confirmed that hybrids had the best stability performance, even more stable than Elands. The males and females performance was average with the male gene pool being more stable than the female one. The sprouting trial revealed that the male gene pool mainly contributed to the poor sprouting tolerance of the hybrids. Combining males and females with good sprouting tolerance provided tolerant hybrids. This was also true for HFN. The method, to evaluate sprouting, was also revised and should be applied to ensure that true tolerant types are selected and to exclude environmental affects.

The Analysis of Variance (ANOVA) regarding the sprouting trial revealed highly significant differences for genotype and year, as well as the interaction between genotype by year. The male gene pool mainly contributed to the poor sprouting tolerance of the hybrid. With so many influences contributing to the variation in pre-harvest sprouting and HFN evaluations, special selection techniques should be incorporated, *e.g.* to exclude environmental effects. In addition, at least more than three years sprouting data generated, under field conditions, is needed to produce accurate data or sprouting scores. Data used from rain simulation facilities, gathered from interval sampling (physiological maturity (FM), 7 days, 14 days, 21 days (21D) after maturity) could supply accurate and repeatable data especially when cut from 14 and 21 days respectively after physiological maturity. It can be concluded that effects of the environment were excluded from the actual sprouting scores obtained from treatment four (FM+21D), reflecting the true sprouting status of the genotypes which are not masked or influenced by year or seasonal effects. Overall, year did not change the genetic trends the genotypes showed. This was not true for the HFN values, as year had a significant influence on the expression of HFN values. Two different trends were observed for the characteristic during the two years of testing. By knowing the parents and the effects of heterosis on the quality characteristics, it would be possible to predict good quality in hybrids.

Distinguishing heterotic groups

Experience gained from the maize model, suggests that hybrid wheat breeding should evolve from two different populations (figure 1). Therefore, Perenzin *et al.* (1996), suggested that the basic requirement in hybrid breeding was to optimize genetic diversity between female and male gene pools. To maximize genetic diversity between the two populations, breeders must be careful to only include germplasm originating from populations which are distinct from each other. They also acknowledged that knowledge of the relation between the germplasm sources could be based on the origin of the germplasm, pedigree information of the lines concerned, and observed differences in morphological characters. According to Perenzin *et al.* (1997) kinship relationships based on the coefficient of parentage could be used to detect relatedness between populations. However, they suggested that there were more sophisticated biotechnological methods available to make reliable determinations. They found that when parents were assayed for random amplified polymorphic DNA (RAPD), the results obtained, indicated that the genetic distances could be used to predict hybrid performance. However, these results are in contrast with the results reported by Dreisigacker *et al.* (2005). Perenzin *et al.* (1996), found that parental diversity *per se* was found to be poorly correlated with hybrid performance, and they were not able to predict heterotic combinations using RFLP and RAPD markers. Although testcrosses are more practical to access nicking and grouping of germplasm, it is a more time consuming approach. In pursuing genetic diversity the introgression of alien germplasm could play a significant role, making provision for heterosis based on genomic diversity.

In an unpublished study, by Laubscher, on wheat in South Africa, a total of 10 lines sampled from a female population were crossed with 10 lines sampled from a male population (Laubscher, 1984). The lines were regarded as genetically diverse and originated from the Sensako's hybrid breeding programme. The progeny was tested under low yield and seeding rate (5 kg per hectare) conditions. For yield the average effect of the parents accounted only for 37.2% of the hybrid variance while the female x male cross-interaction accounted for 63.8%. This result showed that although the genetic variance within the female and male sets was significant, the performance of the hybrids could not be predicted from the average performance of the parents nor from the parent progeny performance. The 10 best hybrids, selected from this study, predicted a 43% improvement in yield potential. The assumption was made that the potential of the pure line parents were comparable to the then conventional commercial varieties.

This study set the foundation for the present hybrid development programme in South Africa and in retrospect the current hybrid yield potential confirms the prediction which was made then on the cross-performance of the male and female pools (Jordaan *et al.*, 1997).

Although the presence of heterosis for grain yield in a large number of soft red winter wheat was demonstrated by Barbosa-Neto *et al.,* (1997), the observed genetic diversity in that particular study was limited to an average of 88% similarity in RFLP fragments. The narrow germplasm base of the lines used in their study could partly explain the low correlation between heterosis and RFLP distance. However, it was demonstrated by Melchinger (1997) that the genetic distances based on molecular makers, such as RFLPs, AFLPs and microsatellites (SSRs) could be used to: "1) reveal genetic relationships among different germplasm, 2) assign germplasm to groups and subgroups of similar materials, and 3) detect pedigree relatedness between germplasm". On the basis of this information, new heterotic groups can be established or the genetic base of existing groups can be broadened. He also said that such decisions should be supported by additional information regarding the performance of crosses among these subgroups to access their heterotic response which is essential for identifying promising heterotic patterns.

It has also been demonstrated that SSRs is a powerful tool for the discrimination of wheat cultivars and identification of divergent groups in advanced wheat breeding materials (Plaschke *et al.*, 1995; Dreisigacker *et al.*, 2004; Dreisigacker *et al.,* 2005 and Röder *et al.*, 2002). However, no clear relationship between molecular diversity (using AFLP, RAPD or SSR markers) and heterosis was observed in wheat (Liu *et al.*, 1999; Corbellini *et al.*, 2002 and Dreisigacker *et al.*, 2005). In maize there have been contrasting reports with regard to the predictive power of diversity on a molecular level (various marker systems) and hybrid performance (Lee *et al.*, 1989; Melchinger *et al.*, 1990; Reif *et al.*, 2003 and Kiula *et al.*, 2008). Bernardo (1992) showed that this correlation was highly dependant on factors such as the material being tested and the marker–trait linkages available. It is thus appreciated that molecular technologies can play a role in establishing heterotic groups based on genetic distances, but that field data is still needed to determine the best combinations for optimum hybrid performance (Melchinger, 1999 and Reif *et al.*, 2003).

The identification of heterotic patterns should be the start to a hybrid wheat research and development programme, aimed at developing heterotic populations which are broad based, genetically diverse, and with a high yield, disease and quality performance *per se.*

Two ideas to integrate and probably to be developed further are:

1. This is really critical because when comparisons are made between wheat hybrid selection status and maize hybrid breeding, today, there is a gap to fill. The

recent development of high throughput molecular markers should increase the understanding of wheat heterotic pools. In the near future, the wheat genome sequence will be known, which will also reinforce this technological improvement.

2. Development of so-called synthetic wheat, especially using the very rich eastern allelic distribution of *Aegilops taushii*, may generate a very useful new heterotic pool.

According to Heisey *et al.* (2002) separated cultivation of populations in maize and other allogamous crops such as rye, assisted in their classification into different heterotic groups. They were mainly categorized according to their evolutionary history and geographic origin. In contrast, heterotic groups are not available or so easily distinguishable in wheat, due to their past breeding history. As for other crops such as autogamous crops, breeding of pure line cultivars has relied on deriving transgressive segregants from crosses between complementary parents obtained through a relatively widespread exchange of germplasm. Furthermore, introgression of genes to incorporate new sources of resistance or tolerance regarding various biotic and abiotic stresses from wild relatives of wheat into modern cultivars, contributed to a mix of germplasm from diverse genetic origins (Dreisigacker *et al.*, 2005).

The use of two heterogenic growth types caused difficulty with the nicking of the male and female in the production process. The Sensako hybrid breeding programme had mostly facultative to winter female growth types and very strong winter growth type males. The males had very high levels of rust and disease resistance as well as resistance to Russian wheat aphid. In a recent quality study by Van Eeden (2009) it became evident that the females were of good quality and that males were of less acceptable quality. This was due to the fact that the female program was part of the conventional winter breeding programme and underwent strict quality selection.

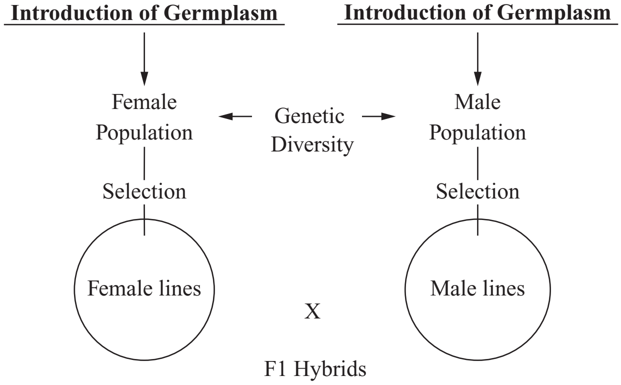

Figure 1 ■ Model for hybrid wheat breeding as suggested by Jordaan (1999).

Selection of female and male parents (Intra population improvement)

Female pool

Procedures and technology to develop pure lines are well-known and are also applicable in the development of female and male lines to produce hybrids. If the final objective is to produce hybrids that are also adapted to low yielding environments, then selection in parent development should be ruthlessly done, sampling the target environment. To have a meaningful discussion on the selection of parents, the structuring or modeling of such a program should be known. According to Jordaan (1999), five different levels of selection can be identified within the female development programme (figure 2).

1. Selection of germplasm to be included in the female pool. Base on: maximizing diversity for the female pool as determined by means of pedigree analyses, marker assisted selection and testcross performance. Identify and improve female characteristics such as the duration of receptiveness of the stigma to pollen and quality of the seed. Select for resistance to biotic and abiotic stresses which could complement characteristics from the male side (Jordaan, 1999). Total sterile spikes and a floret can be seen in figures 3 and 4 respectively.

2. Selection of germplasm from the female pool to be included in the crossing block. Emphasis should be put on recombining new germplasm sources which exhibit excellence, with female lines performing well in hybrid combinations. Focus should be on those crosses which promised to provide the highest frequency of desired progeny (Jordaan, 1999).

3. Developing pure female lines. This stage must include the normal selection techniques encountered in the development of conventional pure lines. It would,

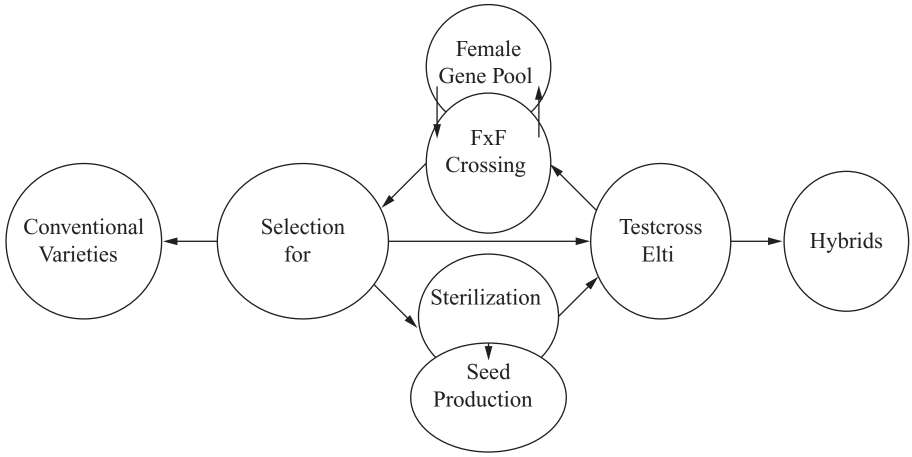

Figure 2 ■ A Model for a female (F) development programme as illustrated by Jordaan (1999).

Figure 3 ■ Totally sterile female spikes.

Figure 4 ■ Example of a totally sterile floret.

however, be a priority to advance lines through the selection phases as quickly as possible, to make an assessment on combining ability with the male lines. Haploid breeding is a valuable tool to achieve homozygosity, as soon as possible, before test crossing the lines. If the production area varies in yield potential, a shuttle programme may be implemented, alternating selection nurseries from high to low yielding potential. In the Sensako development programme, an objective is to raise the level of performance in the female lines to equal the performance of conventional lines at the same level of inbreeding. Pure lines from the female programme could also be released as conventional varieties, depending on whether a release policy of the breeder allows for the commercial release of only hybrid varieties or not. Female lines from the Sensako programme are also tested in trials, to assess their own performance.

4. Selection for cross performance. It is necessary to change the self-fertilizing habit of the wheat plant to produce hybrid seed. This could be done by producing male sterile plants (Jordaan, 1999). For years hand emasculation has been the only method to facilitate crossing, and still is in the Sensako hybrid wheat breeding programme, because using CHA proved to be unsuccessful. Hand emasculation is a time-consuming activity and limits the amount of seed which can be produced and thus, the number of crosses which can be made. The amount of seed per cross was the major limitation in accessing the value of hybrids and also disqualified F1-hybrids from commercialization (Jordaan, 1999). Female lines are selected on the basis of the performance of their test crosses. These test crosses are replicated in trials at sites which represent the target area. Selected lines are being retained for further selection, backcrossed to CMS, or in the case of CHA used as parent for producing hybrids, and are finally also recycled in the female pool as parental germplasm.

5. Selection for female characteristics. Female characteristics are those which relate to the hybrid seed production process. Although, not important in hybrid *performance*, there may be critical attributes in the commercialization of hybrids. In the case of the CMS-system, the B-line must be a good pollinator and should shed enough pollen over a long enough period to ensure good seed sets on the sterile component (A-line). Trapping of anthers within the glumes is a stress related character and should be selected against. Furthermore, there are large differences among stigmas of female lines for their ability to stay receptive to pollen over several days, especially under warm, dry weather conditions. A higher seed set on the female relates to better seed quality, while a low seed set is usually a distinctive feature of poor seed set or might be a characteristic of the female involved.

During the 2003 wheat season, foreign germplasm was obtained from Dr Maarten van Ginkel from the CIMMYT wheat breeding program in Mexico. This material is known as "*multi-ovary*" and may provide an opportunity to improve seed set values in the female pool. When pollination of an individual floret

Figure 5 ■ Multi-ovary phenomenon.

occurs, a total of three seeds are developed, per floret, instead of the normal one seed per floret (see figure 5). Work to date suggests that the characteristic is controlled by recessive genes and should not be expressed by the F1 hybrid. Some of this material has now been introgressed into some of the female backgrounds and the first double haploid lines will be evaluated under field conditions during the 2010 production season. The seed, produced using this material is of moderately poor quality but hybrid wheat farmers in South Africa are used to planting F1 seed of moderate seed quality.

Male pool

The rules which apply to the selection of male germplasm remain the same as in the case of selecting for female germplasm. The technology and selection methods used for the development of male (M) lines depend on the availability of a CHA. When available, recurrent selection producers are possible. For CMS the use of the female tester line is not a practical option, since all crosses would have to be made by hand, or in isolated cross pollination blocks, for every individual cross. The strategy should rather be to identify the core M-lines, or germplasm, and introduce unique characters, by means of backcrossing, to a genetic background known for its cross-performance to the Female pool. The emphasis should be on developing males which restore the CMS in the female. The genetic factor for fertility restoration (R-genes) could be included in males by means of backcrossing. However, if the males have the normal cytoplasm it would be necessary to make testcrosses on lines having the *Triticum timopheevi* cytoplasm to detect the R-genes. The practical option would be to select males segregating for the R-genes in the background of the *Triticum timopheevi (Tt)* cytoplasm. Hence, every plant is a test cross and allows the strategy for selection of the Male germplasm under stress conditions such as insufficient water and high temperatures, which are known to inhibit the expression of fertility restoration (Jordaan, 1999). In figure 6 the good pollen extrusion attributes of the male line can be seen.

Figure 6 ■ Good pollen shedding properties of the male line.

A gene which expresses improved pollen extrusion has been discovered in rice, which if used in wheat breeding programmes could generate a new type of male, with improved pollen extrusion capabilities.

Structure of the South African hybrid breeding programme

Breeding of commercial hybrids at SENSAKO is based on the *T. Timopheevi* cytoplasmic male sterile system (CMS) and a genetic fertility restoring (R) system. Genetic diversity is paramount in a hybrid breeding programme for maximum heterosis and two diverse breeding populations are developed with maximum inter-population cross performance.

The female genepool development concentrates on the use of spring derived exotic germplasm and agrotypes with quality selections being carried out in accordance with South African germplasm requirements. Synthetic lines are used as the source for breeding disease resistance in the females. Tugela-DN, a South African wheat cultivar, donates the aluminium tolerance required for the female genepool.

The male genepool has a narrow base and originates from hard red winter derived germplasm with very good yellow rust resistance. A foreign aluminium toxicity donator is used for the breeding of acid soil tolerance. Special attention has been given to breed sprouting tolerant males as this was a major cause of concern in the breeding of hybrids. Locally a quality source is used to incorporate bread making quality.

An intra-selection programme has been devised within the F2 to the F6 populations, in both the separate male and female segregating populations. From the advanced F4 and F5 male and female populations, combining ability is tested from inter-selected males and females and the offspring is tested in the following year. The males are tested on the best commercial females and the females on the top performing commercial males.

The female programme consists of a B-line and A-line stream. The best selected B-lines go into a backcross programme where the CMS is transferred in order to develop its A-line and it is carried out by means of single paired plants. These plants are evaluated in the field and the A-line checked for complete sterility. In this same manner A-line productions are maintained while paired plants are planted together with their paired B-lines.

The best pure line male performers from the yield trials are included in scaled trials where the males are planted on different planting dates/at interval planting to pollinate the sterile commercial female. The offspring are weighed and again the yield performance of the offspring is tested in either the winter or facultative performance yield trial at different locations. Within these scaled trials the females are selected for long stigma receptivity and good seed quality. The males possess good pollinator qualities with long duration and high quantity of pollen production. Anther emergence is also evaluated and males must exhibit good fertility restoration. In order to improve the production ability of the hybrid cultivars, taller males are selected as well as shorter females.

Other known existing programmes

The current existing hybrid wheat breeding programmes in Europe are the legacy of the last 30 years invested in hybrid wheat breeding. There has been a long history over this period of starting and then subsequently closing programmes. The market shares of hybrids in countries where they are currently sold, are still very limited and frequently in the range of 1 to 3%.

The different countries which still have some activity in hybrid wheat breeding are summarized as follows:

– **Australia**: 40 000 ha until 2001/2002. Since then, no hybrid wheat sales have occurred due to disease pressure. The company AGT, part owned the Limagrain group, is the only seed company involved in hybrid breeding;

– **China**: Less than 100 000 ha in 2009, with various public role players;

– **India**: 34 000 ha, with the cultivar Mahyco covering 100% of the current market share, but JK Seeds and the public sector also are investing in hybrid wheat programmes;

– **South Africa**: 23 000 ha in 2008, Sensako is the only role player;

– **Europe**: Nordsaat is the sole role player with partnerships with the main conventional breeders namely:

- *France*: 95 000 ha in 2006/2007, 125 000 ha in 2007/2008 and 2008/09,
- *Germany:* 20 000 to 30 000 ha,
- *Central Europe*: a few thousand ha.

Hybrid wheat economics

The successful adoption of any hybrid crop requires that a certain level of economic profitability be met. Wheat is historically cultivated as a self-pollinated crop and requires a level of economic justification similar to other hybrid crops, much like corn and sorghum, if it is to be widely adopted. For the present time, hybrid seed costs more than certified varietal seed or farmer-saved seed (Carvis and Cooper, 2009). In South Africa the cost for hybrid wheat is roughly 1.3 times higher than that of the commercially available open pollinated cultivars.

According to Carvis and Cooper (2009) the economic threshold for the acceptance of hybrid wheat is a complex function of a number of factors beyond the additional quantity of grain produced by the hybrid. They identified the critical factors as:

1. Hybrid advantage, such as yield stability, pest protection and agronomic traits important in any specific hybrid versus cultivar comparison;
2. Average purchase price of hybrid seed versus varietal seed;

3. Anticipated commodity price of grain, or other market factors;
4. Expected return on the hybrid seed investment by the grower;
5. Seeding rate of the hybrid versus the cultivar;
6. Risk of crop failure due to natural disasters.

The commodity price of wheat influences the relationship between the hybrid advantage and the expected or actual return on investment. Lower hybrid advantage requires a higher market price to generate an adequate return on the seed investment. On the other hand, a greater hybrid advantage still gives an attractive return at a lower market price. According to Carvis and Cooper (2009) a number of models exist, which suggest that an economic threshold for converting from self pollinating cultivars to hybrids requires a hybrid yield advantage in the range of 0.65 to 1.0 tonnes/hectare, generating a return-on-investment ratio of 1.5 up to 2.0 times. Several of the factors affecting the economics of hybrid wheat are discussed below.

Seed production issues

Wheat is a self-pollinated inbred crop, has perfect florets, limited supplies of pollen, and a relatively brief period of stigma receptivity. Hand emasculation is impractical for commercial seed production, but cytoplasmic male sterility allows production of hybrid seed on a field scale. Seed yields of productions are normally very low and combined with high seeding rates for commercial productions. It is difficult in this scenario to establish a proper profit from seed sales, and normally the selling price for hybrid seed of companies exceeds what producers are willing to pay (Duvick, 1997b).

The biggest obstacle for hybrid seed production is the conventional procedure used to produce hybrid wheat seed, viz. to plant alternating strips of male and female parents, where the male, by mechanical or wind means, pollinates the female. Wilson (1997) reported that this is moderately efficient, resulting in seed-set values of the female that vary between 50 and 80%. He also claimed that it is also a costly method because it requires cautious, separate planting and harvesting of the two parents and some productions even use unproductive separator strips. A key factor causing incomplete seedset is the difficulty in effectively moving wheat pollen, from the male to the female, over a distance (Wilson, 1997). According to Bonjean (personal communication), when ropes are used in China, as a mechanical form of dispersing the pollen equally in most hybrid rice productions, increased seedset levels of up to 15% are observed (figure 7). However, the timing for carrying out this procedure is very critical. In India (Mahyco) it seems that a good "know-how" in this regard, has been developed. Small fields, in India, with male and female rows of only 3 m in width, seem to favour the pollination process. In Australia helicopters are used but it is not cost effective.

In order to increase the success ratio of seed productions, they are normally performed in areas where conditions favour high productivity; this approach

Figure 7 ■ Rope usage to improve pollen dispersion in China, as it has previously been done in hybrid rice.

eliminates the biggest risk factor that can influence hybrid seed production, namely water availability. With the latter goal in mind, most of the hybrid productions in South Africa are being carried out under overhead irrigations systems. The average yield of irrigated wheat varies between six and seven tonnes per hectare. When lower yield levels are obtained, in hybrid seed productions, the farmers must be compensated for loss of income compared to planting commercial open pollinated cultivars. This drastically increases production costs. As the irrigation areas are also far from the processing plants additional handling, storage and transport costs need to be accommodated.

Wilson, (1997) proposed that hybrid blends should be made between the male and female in a 20:80 ratio respectively, resulting in an increase of 10% seed set in the female. The yield levels of the male, however, had an effect on the performance of the F1 hybrid. In Australia, seed production is being done using blends between females and males. These blends often produce 60%, and more seed, compared to original hybrids. However, the yield of the female still yields 40% less than the male (personal communication, source AGT). Results of a blend versus strip hybrid wheat seed production which verifies the previous statement, at two Australian localities, namely Tamworth and Carrabin, during the 2005 production season are shown in table 8. Similar results were obtained by Bo jean some years ago in Europe. Regarding such blends, the quality characteristics of the male as well as the hybrid must be very similar in order to convince farmers and agro-industrialists to use such a variety. Currently Signet is in the process of commercializing such a barley hybrid in the UK (Bonjean, personal communication). In South Africa this suggestion will be difficult to achieve because of the huge difference in growth period between the male and female. An alternative option would be to introduce the herbicide dominant resistance in order to remove the male line.

The incorporation of *Roundup Ready* or *Clearfield* technology into the female but not into the male, would enable growers to eliminate most male plants from the hybrid crop using normal weed control procedures. When Sensako was still part of Monsanto, we embarked on this route during 2001. Before the female material in which the Roundup ready gene was incorporated, could be sent to South Africa for regulatory tests, a business decision was taken not to continue with the project. Clearfield technology is not part of GMO technology and use of this would eliminate additional costs for applying for regulatory approval, thus making it a more attractive option.

Barnabás (1973) developed a purple hybrid seed production system, in which the restorer parent has purple grain colour, while the female has normal white or brown coloured seed. The seed of CMS and *Rf* parents were sown mixed, thus improving the chances of pollination. The purple-coloured grain produced on lines with the *Rf* marker was separated, using in the mixed harvest, using a colour selector. Due to practical and financial reasons this approach was not considered a viable option.

Table 8 indicates the difference between the two production methods was less with the better cross-pollinating parents and the higher ratios of male to female. However, one must keep in mind that the narrow experimental strips would tend to improve the cross-pollination compared to commercial strip widths of around 10 m.

Without significant progress in seed production, the development of hybrid wheat will be difficult to commercialize on a large scale, despite its superior agronomic performances.

Table 8 ■ Results of blend versus strip hybrid wheat seed production at Tamworth and Narrabri, 2005.

Location	Cross type	Ratio male/female	Yield of female ton/ha	Yield of female as % of male	% increase with blends
Narrabri	Strip	20/80	0.776	39.30	
Narrabri	Blend	20/80	1.409	71.3	81.5
Tamworth	Strip	20/80	0.504	20.8	
Tamworth	Blend	20/80	1.109	44.6	120.3
Narrabri	Strip	33/56	0.931	47.1	
Narrabri	Blend	33/56	1.409	71.3	51.4
Tamworth	Strip	33/56	0.912	36.5	
Tamworth	Blend	33/56	1.445	56.8	58.4
Narrabri	Strip	50/50	1.101	55.7	
Narrabri	Blend	50/50	1.268	64.1	15.2
Tamworth	Strip	50/50	1.165	46.6	
Tamworth	Blend	50/50	2.004	77.0	72.0
Narrabri	Strip	Mean all ratios	0.936	47.3	
Narrabri	Blend	Mean all ratios	1.362	68.9	45.5
Tamworth	Strip	Mean all ratios	0.860	34.5	
Tamworth	Blend	Mean all ratios	1.519	59.5	75.6
Both sites	Strip	Mean all ratios	0.898	41.0	
Both Sites	Blend	Mean all ratios	1.441	64.2	60.4

Environment

Selection efficiency is restricted by the extent of the interaction between the environment and the genotype. A large number of factors interact to reduce yield. Some are fixed variables while others are manageable, but of most interest to the breeder are those derived from weather conditions and which cannot be predicted in advance. These include factors such as the amount of precipitation, the distribution thereof, soil moisture, temperature, etc. Attempts by wheat breeders, to incorporate genetic stability to these variables, were contrary to the progress which had been made to develop wheat varieties with yield potential. Progress was made in developing varieties performing under inadequate moisture and unfavorable temperatures, even when the plant's response to such conditions was not fully understood or elucidated by physiological and biochemical processes. Conditions of water stress defines a stress environment which is usually also characterized by periods of high temperature, resulting in a drought phenomenon (Jordaan, 1999).

The proper choice of a production location will have a significant impact on both the stability and the yield of hybrid seed production and the resulting cost of hybrid seed. Experience has shown that lower costs for hybrid seed production generally will be obtained under high-yield conditions associated with irrigated production areas and reliable wind patterns during the pollinating season. In addition to the obvious requirement for wind to move pollen from the male to the sterile female plants during anthesis, ideal production locations also have the following characteristics:

1. Consistency of production, including infrequent late frosts, hailstorms and other natural disasters, and with a low precipitation pattern during the CHA application and pollination periods.
2. Lack of diseases, especially head or ear blights and other diseases which may affect seed quality.
3. Lack of prevalent noxious weed problems or conditions that favour carry-over of volunteer wheat.
4. Logistically near seed conditioning facilities and distribution centres to help reduce freight costs.
5. Cooler environments (higher altitudes) often seem to have better seedset, presumably due to increased pollen viability and reduced stress on the crop.

Hybrid and winter wheat are produced in the dryland areas in Southern Africa, which over a ten year average period produced yields of 1.18 tonnes per hectare. Therefore, it can surely be described as one of the lowest yielding environments on which wheat is being grown commercially. This environment can be compared to Quizenberry's environment one, with elements of environment two (Quizenberry, 1981), where wheat is usually grown on only the available moisture in the soil, which was conserved from rains that fell during the preceding summer months. The crop usually grows without any rain up to heading. Thereafter, it receives rain in variable quantities up to maturity. During this period the wheat plant is usually under water stress which might be worsened by spells of high temperatures. Factors such as soil depth, soil type and agronomic practices interact with the availability of water and create an ever changing environment, which is not predictable. Specific agronomic systems are prescribed by the water status in the topsoil at planting time. Dry topsoil might be as deep as 15 cm at planting time and requires a specific plant and planter technology. Accordingly, yield conditions will vary from a high potential to a very low potential (Jordaan, 1997).

Jordaan (1996) has delivered evidence showing that hybrids perform well in dryland stress environments in South Africa. Bruns and Peterson (1997) as well as Peterson *et al.*, (1997) gave similar convincing evidence on the performance of hybrids in the Great Plains of the USA. They ascribed the improved performance of hybrids to the inherent yield stability which is associated with hybrid wheat cultivars. Hybrids have higher regression slopes and lower deviations from the regression of pure lines. They attribute this higher stability of performance to factors such as heterosis for green leaf duration, improved heat tolerance and disease resistance. They utilized computer programmes to match exclusive traits of the parents in hybrid combinations in order to improve agronomic expression.

Planting configuration and nick adjustment

Production fields are currently planted in alternating strips of female and male parents with either CMS or CHA hybridization methods. Experience also dictates that, when possible, these strips must be planted at right angles to the prevailing wind pattern which occurs during the anticipated pollination period in order to improve pollination success. The actual width and resulting ratio of female to male strips are often determined, in large, by the width of the commercial planting, spraying and harvest equipment available to the producer. Care must be taken to prevent accidental mixing of the male and female seed from planting right through to harvesting. Generally narrower and more frequent male strips permit higher ratios of female to male, which improve the pollination effectiveness and results in more hybrid seed production per total area. According to Carvis and Cooper (2009) typical female to male ratios, in production fields, in the Great Plains of the United States are in the 2:1 to 4:1 range. In South Africa a 3:1 ratio is used. Male planting widths from 1.5 m up to greater than 6.0 m have been tried in combination with female strips from 3.0 m up to 20 m wide. Under South African conditions male and female planting widths are 2 m and 6 m respectively. Their experience has shown that hybrid seed set typically begins to drop off sharply more than 12 m from the source of pollen. However, environments with less wind than the Great Plains region, of the United States, may require lower female to male ratios and a narrower width of the female parent. There have been reports in the US with the CHA "Genesis" during the 1998 season where seed yields on approximately 3000 ha, which was sprayed, averaged more than 3000 kg/ha, and seed yields in France, on a similar area, averaged more than 5000 kg/ha (Carvis and Cooper, 2009).

Maximum hybrid seed set for a given hybrid combination will occur when the lemma and palea of the female are open with a receptive stigma at the same time that the male is shedding pollen. Under normal circumstances this requires that the male must flower two to five days later than the female to achieve optimal flowering coincidence (nick). Carvis and Cooper (2009) reported that flowering data, including the number of days to 50% pollen shed (on the male side) and number of days to 50% flower opening (on the female side), and seed yield data were collected in top-cross nurseries over a nine year period by the HybriTech US soft wheat programme. They determined that the nick had to be calculated as the day of 50% pollen shed minus the day of 50% flower opening. Hybrid seed yields were optimized when flowering nick was plus two or three days pollen shedding, although commercially viable seed yields with wider or narrower nicks have been obtained (Carvis and Cooper, 2009).

Females are often planted at higher populations than males to reduce tillering and minimize differences in growth stage for optimal nicking efficacy. In contrast some males will respond to a somewhat reduced seeding rate by the production of secondary tillers, thus both delaying and spreading the pollen load over a greater period of time to ensure greater likelihood of a favourable nick. The excellent tillering capacity of South African hybrids can be seen in figure 8. At low seeding rates each plant can produce more than 30-40 tillers. Carvis and Cooper (2009) said that it would be difficult to get a very large adjustment in the nick of the female and male by staggering the planting dates, where cereals in the United States are sown in the fall (autumn). A one week delay in planting in the fall often translates into only a one or two-day later flowering date the following spring. Delayed planting would bring an associated risk of poor establishment – thus increasing the threat to seed production capabilities. The breeder has to take the decision as to balance these two issues to minimise the risk of low seed sets. They suggest that staggered plantings, to adjust nick, are a more practical solution for spring-sown cereals, but this can also be limited by day-length sensitivity genes that are more common in spring wheat. Many other techniques, such as burning or mowing of the male and differential fertilizer application, have been attempted to adjust the nick between females and males. All of these have met with varying

Figure 8 ■ Individual hybrid plant demonstrating excellent tillering capacity.

degrees of success, but they also add to the cost of hybrid seed (Carvis and Cooper, 2009). In South Africa varying the seeding rates of the males to produce more and delayed tillers to expand pollen shedding period has been used. The male strips are planted at different planting dates to obtain better pollination levels.

Temperature plays an important role in achieving optimal vernalisation requirement. Hybrid seed production must be planned accordingly in order to satisfy the vernalisation requirement of the hybrid parents otherwise optimal "nicking" will not be achieved, with consequential poor seed set. Figure 9 displays the variation of the temperatures which occur in a normal year in South Africa. Although the data dates back to 1997 and 1998 it does illustrate the temperature patterns which occur during a normal season under field conditions. This plays an important role in meeting vernalisation requirements.

Figure 10 shows the effect when vernalisation requirements are not fully satisfied. These rows will take much longer, or never, reach maturity.

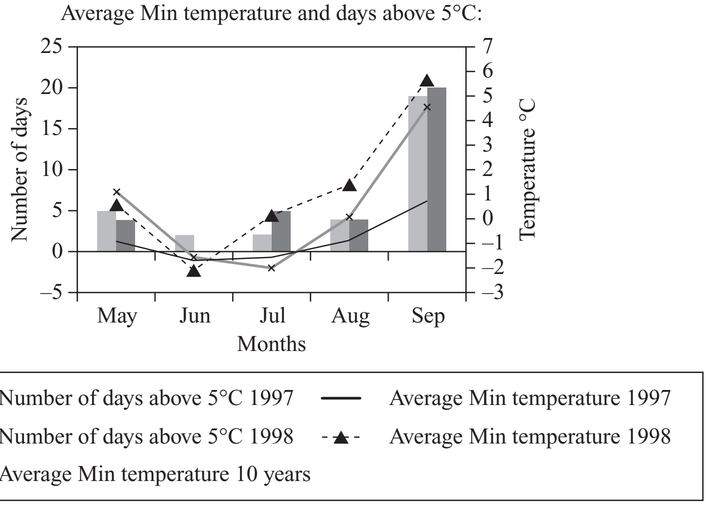

Figure 9 ■ Average minimum and maximum temperatures from May to September.

Figure 10 ■ Slide of vernalization requirement not satisfied.

A study was initiated by Sensako with the main goal to determine the receptivity of the florets of the female lines A 966 and A 972. The obtained data should provide a solution for the poor seedset values of SST 972. Spikes of both female lines were cut and bagged at growth stage Zadoks GS55 under greenhouse conditions. Three treatments were used (intact, one side cut and both sides cut spikes) for each of the CMS lines regarding both hybrids namely SST 966 (A966) and SST 972 (A972). Pollination occurred at two day intervals. The results obtained are illustrated in figure 11. The results, for one side cut, followed the same tendency as for both sides cut except that the amount of kernels formed was halved. To make figure 11 less complicated, only the results for both sides and intact spikes are given.

From figure 11 it is evident that the lack of female receptiveness of A 972 is the biggest obstacle in obtaining acceptable hybrid production levels. The treatment for both sides cut, produced almost similar amount of kernel per spike than the intact spikes of A 966.

A study was conducted by the Sensako hybrid breeding programme to determine the influence of planting splits on the yield performance when producing SST 966 and SST 972 hybrids. The results are summarized in table 9.

From table 9 it is clear that the best split for producing SST 966 was obtained when the female were planted between 17 and 25 May and the male on the 12th of June. This implies a split of almost 17 to 26 days. The best results for SST 972 were obtained when the split, between the female and male, was eight days apart. With

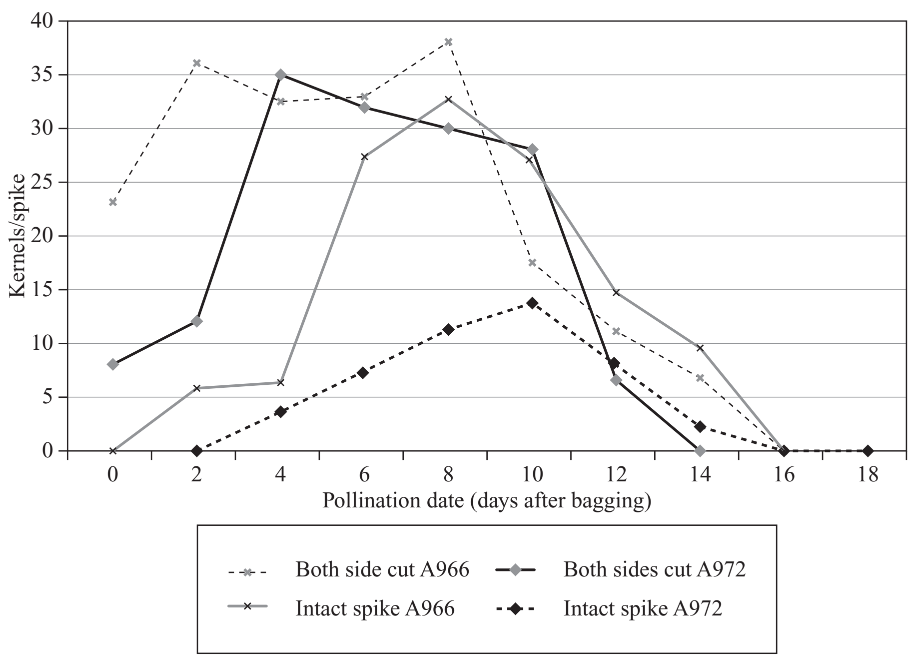

Figure 11 ■ Mean receptivity levels from A 966 and A 972 florets.

Table 9 ■ Influence of planting splits on the female yield in the production of SST 966 and SST 972 for the 2003 production season at Lichtenburg.

	Male used R41	**Male used R41**
Planting split#	**A 966 yield ton/ha**	**A 972 yield ton/ha**
0*:1	1.47	1.60
0:8	1.12	2.51
12:0	2.12	1.38
17:0	2.72	1.59
26:0	2.76	0.77
CV %	18.7	19.7
LSD 95%	0.81	0.74
R^2	0.4	0.36

* = Male is indicated as 0 # = Planting dates applicable: 26:0 = 17.
May; 17:0 = 25 May; 12:0 = 31 May; 0:1 = 13 June and 0:8 = 20 June. Male was planted on 12 June.

this wide variation in splits necessary to construct a proper nick, taking into consideration that this was for only one male, locality and season, it is understandable that the latter will considerably influence the outcome of a successful production.

Figure 12 shows different row spacing at a similar seeding rate of 5 kg per hectare for SST 972.

In South Africa the use of wider rows relates to the depth of the dry topsoil layer. The deeper the dry topsoil layer, the more dry topsoil must be pushed away to plant seeds into moisture, and the wider the rows have to be. This technology has already been adopted in practice and is not based on theory. Seeding rate within the rows varies with planting date, maturity of the variety, soil water status and very seldom exceeds 30 kg per ha^{-1}. Reports on the effect of row width (Paulsen, 1987) and the effects of seeding rate on yield and yield components (Frederich and Marshall, 1985; Bulman and Hunt, 1988 and Royo and Ramagosa, 1988) describes interactions and correlated responses in non-stress condi-

Figure 12 ■ Row width and a standard seeding rate for SST 972.

tions. Reports on the expression of heterosis for yield, and also on the expressions thereof in yield components associated with final yield, are inconsistent (Virmani and Edwards, 1983; Pickett, 1993; Borghi and Perenzin, 1994; Martin *et al.*, 1995; Larik *et al.*, 1995; Uddin *et al.*, 1992; Menon and Sharma, 1994; Winzeler *et al.*, 1994; Sharma *et al.*, 1991 and Liu and Li, 1994).

Engelbrecht (Unpublished PhD study, 1991), describes the deviation of a hybrid from the mid-parent value (according to the definition of heterosis) for yield and yield components at different row widths (25 cm, 50 cm and 75 cm) and three different plant populations (15, 30, 50 plants per m^2) at different localities and seasons under South African conditions. These row widths and plant densities relate to cultural practices in the specific low yielding environment in South Africa. The expression of heterosis, although inferences are limited to one hybrid and its two inbred parents, is significant for all the main variance components and interactions. The biomass production per m^2, number of ears per m^2 and 1000 kernel weight are highly correlated with yield and significant heterosis is expressed. Interaction between row width and plant population has determined that the hybrid's advantage is a specific adaptation to yield potential. In narrow rows the expression of heterosis is higher at the high plant densities and better adapted to high yield potential, while in wider rows the deviation from mid-parent values is the highest at low seeding rates when the mid-parent values are low (low yield potential). Clearly the hybrids relative performance relates to space arrangements of plants at specific row widths and plant population, supporting the conception that, for the older generation hybrids, the magnitude of heterosis is yield potential specific and can be optimized by agronomic practices. The hypothesis, of wider rows and low seeding rates for low yielding environments, seems to hold in practice.

Under these conditions (wide rows, 75 cm, and low plant population, 15 plant m^2) the biggest contribution to hybrid grain yield, stems from the number of spikes m^{-2} (rg = 0,57) and the number of spikes per plant (rg = 0,53). In both cases the relationship was not sensitive to narrow rows or higher populations (Engelbrecht, 1991). In the yield limited environment, kernel weight made a significant contribution (rg = 0,43) to higher yields, although less in narrower rows and higher populations. The contribution of grain weight, which has showed significant heterosis irrespective of row width and population density, might be an important phenomenon stressing the importance of heterosis under stress conditions, since the phenological stages when this component is produced (Slafer and Rawson, 1994). This coincides with the occurrence of drought (depletion of soil moisture and high temperatures). Thus, the lower plant density in wider rows, together with the insufficient soil moisture, creates a situation where the environment satisfies the requirements of assimilates for grain growth. The role which the wider rows and low seeding rates play in light inception should be investigated and also the effect of air flow in cooling down the canopy during periods of high temperatures. The underlying processes of physiological traits affecting yield potential have been thoroughly discussed by Slafer *et al.*, 1996; Blum, 1996; Richards, 1996 and Araus, 1996.

Harvesting and seed conditioning

Female and male strips must be kept separate during and after harvest. While it may be possible to remove the male strips after pollination, the loss of this grain would add to the cost of production of the hybrid seed. The typical practice is to completely harvest the grain in the male strips prior to starting the harvest of the hybrid seed in the female strips. This minimizes the chance of contamination of male seed with hybrid seed. Figures 13 and 14 illustrate a typical hybrid seed production with adjacent male and female parents in South Africa (under dryland) and in China (under overhead irrigation) respectively.

Cleaning and conditioning of hybrid seed is essentially the same as for a certified crop of varietal wheat seed. First-generation and some second-generation CHAs had a tendency to produce shriveled seed. Newer compounds generally produce seed that is sound and visually similar to self-pollinated seed produced in the same environment. On occasions, hybrid seed can be larger than untreated seed. Larger seed can be a result of having a reduced sink capacity in plants with reduced seedset. Large seed size, while generally favourable to seedling vigour

Figure 13 ■ Hybrid seed production under dryland conditions in South Africa.

Figure 14 ■ Hybrid seed production under overhead irrigation conditions in Australia (AGT).

and growth, can add to the cost of goods and reduce the economic advantage of hybrids if planting high populations is the prevalent farm practice.

Costs and planting rates

Carvis and Cooper (2009) reported that some experimental evidence exists which suggests that hybrids can tolerate slightly reduced seeding rates when compared to the established local practices for cultivars. Presumably, this is due to better seedling vigour and the ability to support slightly higher tillering capacity than cultivars. In practice, the extent to which most hybrids can respond to lower seeding rates is probably not much lower than 10% when compared to the traditional cultivar's seeding rates for a given area. This is, however, an area which requires more attention.

The low seeding rates (15-25 kg ha^{-1}) recommended in the summer rainfall, winter wheat production agro-ecosystems of the Free State, favour the use of F1 hybrid bread wheat due to yield and performance stability advantages and reduced relative input costs for seed. Hybrids in general, have proved to be more consistent in yield performance over seasons and localities than commercial standard, pure-line cultivars (Jordaan *et al.*, 1999). The same was found with regard to quality stability and hybrids tended to be more stable than the males, females and conventional cultivars. The use of hybrid crops is usually targeted to increase yield in low potential environments. Results from South Africa report that hybrids out-yield inbred lines by 15% at a 2 t/ha average production potential when narrow row spacing and low seeding rates (< 25 kg/ha) are used. The heterosis is maximized in hybrids where the parents are photoperiod sensitive, with little or no vernalisation requirement and the hybrid SST 983 is evidence of this observation. This cultivar was one of the highest yielding hybrids ever released, but due to the low seedset of its female, in the production process, it resulted in a high cost of seed.

The cost effective production of hybrid wheat cultivars in South Africa are illustrated in figure 15. A total of 5 years data was used to construct the graph.

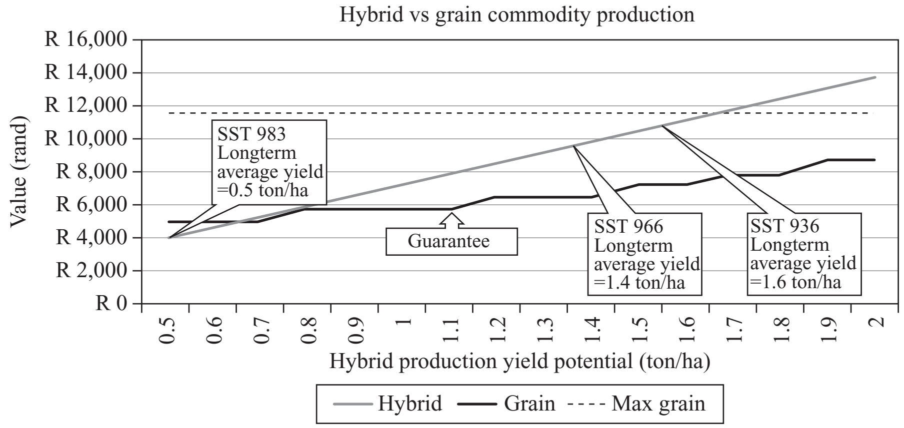

Figure 15 ■ An illustration of hybrid versus commodity price ratio.

The orange line represents the maximum yield limit where yields above this level will not result in improved profit margins. The green line represents the lower limit where yields below this line result in negative profit margins. The blue line is the regression line that displays the profitability of the individual hybrids. From this data it is evident that the very successful hybrid, viz. SST 983, is being produced at a constant loss. Therefore, a hybrid like SST 936 produces the most economical results. The yield of the male is taken as the guarantee level on which yield levels are being set for payments to be made to the producers. Under irrigation 20% of the potential of the male up to a maximum of 5 tons/ha is being considered for compensating the producers, while under dryland conditions it is 30% of the potential of the male up to a maximum of 3 tons/ha. If the yield levels of the male are lower than 3.5 tons per hectare then the guarantee is cancelled because the management of the hybrid producer is below standard. In order to calculate the price for hybrid seed productions in South Africa, four times the current Safex (South African Forex Exchange) price for wheat, is being taken into consideration, to compensate for the lower yield levels of the female.

In figure 16 the commercial economic benefit of the hybrid cultivar Mahyco compared to a local commercial open pollinated variety, in India, is being illustrated. The data was gathered from a total of 1199 farmers representing a total area of 282 hectares over eight localities. From this graph it is clear that Mohyco performed better than the commercial variety regarding both yield and commercial farm income.

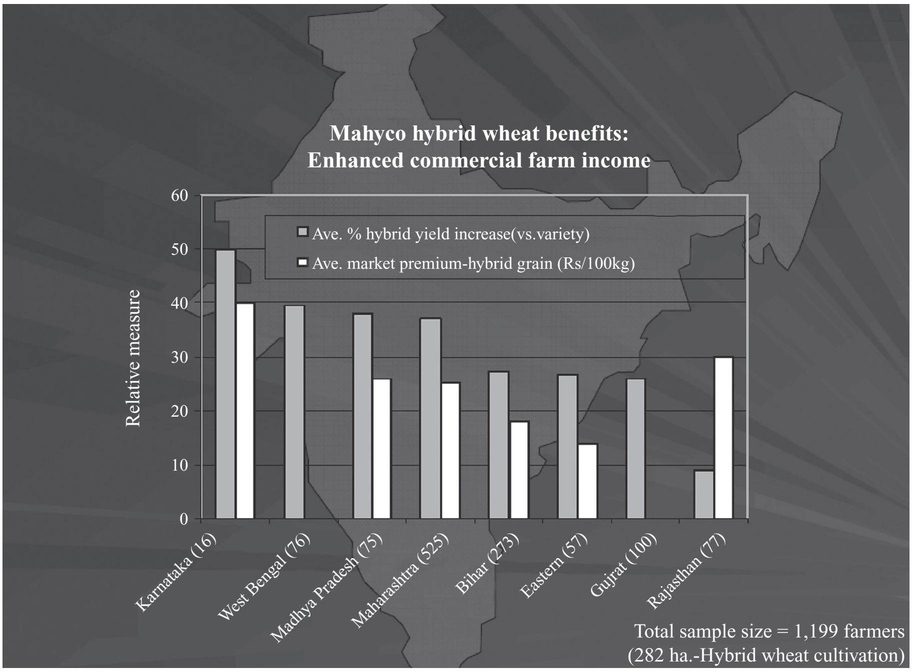

Figure 16 ■ The economic benefits of Mahyco hybrid cultivar compared to commercial open pollinated varieties.

Genetically Modified Organism (GMO) technology in hybrid wheat

The commercial exploitation of heterosis has been one of the driving forces in the rapid and extensive development of privately funded crop-breeding research efforts around the world. Nowhere is this more evident than in the development of privately funded maize breeding in the USA. Today in the USA, almost all the commercial directed breeding efforts aimed at the development of maize hybrids have shifted form public to privately funded research. Other major factors include the market value, the competitive structure and the presence of intellectual property protection systems (Hunter, 1997). The best example is the maize, canola and other breeding programmes of Monsanto. This development of private sector investment has not been realised for wheat breeding and the biggest portion of current breeding programmes are being funded by the public and government sectors. Public acceptance of GMO applications in wheat, would encourage the development of both hybrid and conventional wheat breeding programmes in the private sector.

Wheat is open pollinated and as such farmers have two sources of seed namely, they can purchase commercial seed, or they retain their own grain as seed (Farm save seed – FSS). This means that the price of wheat is extremely volatile, with the result that, if the price of wheat seed increases, farmers retain more seed and purchase less seed. In South Africa there is "farmers' privilege" within the Plant Breeders Rights act, which implies that farmers can retain their seed, but that they may not sell it to other farmers. If it is assumed that a GMO trait in wheat would not be free this would result in an increase in the cost of commercial seed and hence, more than likely, an increase in the amount of farm saved/retained seed, which would potentially lead to less commercial seed being purchased. This will threaten the profit margins of wheat breeding companies. Given that Sensako's route to market is royalty dependant and, therefore, volume dependant it is obviously a concern to Sensako. Sensako's current position is that the farmers are desperate for this technology as they stand to benefit most from it. Before GM wheat is introduced, a model needs to be secured that will provide for the collection of trait fees from both buyers of commercial seed, as well as farm saved seed. With the latter in mind, a hybrid of licensing seed concept can be proposed, much along the Pannar model, instead of selling it. This circumvents the "Farmers privilege" in the PBR act as the seed is not sold, and raises a contractual obligation for a farmer to pay a royalty/trait fee on all seed. Even if the system works in theory, in practice it may not because there is simply too much policing involved. It makes more sense to collect a fee at the collection points, much along the lines of the statutory levy.

Traditionally, seeding rates in the irrigation and Cape production areas are between 110 to 130 kg/ha. Currently farmers are reducing seeding rates to levels between 60 to 90 kg/ha and even lower in some cases. If the seed production issues are being solved by means of the multi-ovary phenomenon and Clearfield technology, hybrid technology can be part of a solution to implement GMO technology as a cost-effective option where the breeder has control over the technology, because FSS seed would not be option anymore.

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