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Original Article

Cytoplasmic Male Sterility–Based Heterosis Breeding for Yield and Quality Improvement in Onion (Allium cepa L.) with Special Reference to Rainy Season Cultivation

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ABSTRACT

Onion (Allium cepa L.) is a globally important vegetable crop valued for its culinary, nutritional, and economic significance. However, onion productivity remains highly unstable, particularly during rainy (kharif) season cultivation, owing to excessive rainfall, high humidity, temperature fluctuations, and severe disease pressure. Genetic improvement through conventional breeding has been slow due to the crop's biennial growth habit, cross-pollinated nature, high heterozygosity, and pronounced inbreeding depression. In this context, heterosis breeding has emerged as a powerful and reliable strategy for improving yield, quality, and environmental adaptability in onion. The discovery of cytoplasmic male sterility (CMS) by Jones and Clarke revolutionized onion breeding by enabling economical and large-scale hybrid seed production, circumventing the limitations imposed by floral morphology and manual emasculation. CMS-based hybrids have consistently exhibited substantial heterosis for bulb yield (30–60%), bulb size and uniformity, earliness, total soluble solids, storage life, and resistance to major diseases such as anthracnose (Colletotrichum spp) and usarium basal rot (Fusarium oxysporum f. sp. cepae). Genetic analyses using diallel and line × tester mating designs have revealed the predominance of non-additive gene action for yield and several quality traits, further validating the suitability of heterosis breeding in onion. CMS-based hybrids are particularly advantageous under rainy season conditions, where they offer superior yield stability, enhanced disease tolerance, uniform maturity, and improved marketable quality compared with open-pollinated varieties. Although challenges such as limited CMS and restorer diversity, environmental sensitivity of sterility expression, and complexities in hybrid seed production persist, recent advances in doubled haploid technology, molecular characterization of CMS systems, and genomics-assisted breeding provide promising avenues for overcoming these constraints. This review critically synthesizes progress in CMS-based heterosis breeding in onion, with special emphasis on rainy season cultivation, and highlights future research priorities for developing climate-resilient, high-yielding, and quality-consistent onion hybrids.

Keywords: Cytoplasmic male sterility, Heterosis breeding, Onion hybrids, Yield stability, Bulb quality, Rainy season cultivation

INTRODUCTION

Onion (Allium cepa L.) is one of the most widely cultivated vegetable crops globally and holds immense economic, nutritional, and culinary importance. It is an indispensable component of diets worldwide and contributes substantially to farm income, employment generation, and livelihood security in vegetable-based production systems (Anonymous, 2016; Griffiths et al., 2002; Brewster, 2008; Index Box, 2024). Owing to its year-round demand and wide adaptability, onion occupies a prominent position among vegetable crops in both developed and developing countries. India plays a vital role in global onion production, emerging as one of the leading producers and exporters in recent years. In 2022, onion was cultivated over approximately 1.9 million hectares in India, with a total production of about 31.27 million tonnes and an average productivity of 16.3 t ha^{-1} (IndexBox, 2023). However, onion production during the agricultural year 2023–24 declined to 21.97 million tonnes, with Maharashtra (8.60 Mt), Madhya Pradesh (4.17 Mt), and Gujarat (2.06 Mt) being the major contributing states (Department of Agriculture and Farmers Welfare, 2024). Despite its leading position in global

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production surpassing even China in certain years, India's average productivity remains comparatively lower than that of several other major onion-producing countries. This yield gap highlights substantial scope for improvement through genetic enhancement, better agronomic management, and improved post-harvest infrastructure. Onion also holds considerable importance in India's export economy, accounting for nearly 70% of the country's total foreign exchange earnings from fresh vegetable exports (NHRDF, 2018). However, frequent fluctuations in production caused by climatic extremes, disease outbreaks, and post-harvest losses have led to volatility in domestic supply and international trade. Such instability often triggers sharp price fluctuations, affecting both farmers and consumers. Therefore, improving the productivity, quality, and stability of onion production is critical not only for food and nutritional security but also for sustaining export competitiveness and market stability. Among the different production seasons, rainy (kharif) season onion cultivation is particularly challenging and remains the most unstable. High rainfall, elevated humidity, and fluctuating temperatures during the monsoon period create highly favorable conditions for foliar diseases such as anthracnose (Colletotrichum spp) fusarium basal rot (fusarium oxysporum f. sp. cepae) and downy mildew (Peronospora destructor) leading to severe yield losses (Abubakar and Ado, 2008; Ambresh et al., 2013; Sharma, 2016). In addition, adverse weather conditions during the kharif season often result in bolting, delayed maturity, poor bulb development, and reduced storage life, collectively limiting marketable yield and profitability (Mahanthesh et al., 2008; NHRDF, 2018). Genetic improvement of onion through conventional breeding approaches has been inherently slow due to its biennial life cycle, high heterozygosity, and predominantly cross-pollinated breeding system (Jones and Davis, 1944; Veere Gowda, 1988). Early investigations clearly demonstrated that repeated selfing leads to severe inbreeding depression, manifested as reduced vigor, poor bulb formation, and low seed yield, whereas crossbreeding restores productivity through heterosis (Jones and Clarke, 1943; Jones and Davis, 1944). Subsequent studies consistently reported substantial heterosis for bulb yield, earliness, bulb size, uniformity, and quality traits such as total soluble solids and storage ability (Hosfield et al., 1977b; Joshi and Tanodom, 1976; Pal et al., 1988; Evoor et al., 2007). Heterosis breeding has therefore emerged as one of the most effective strategies for improving yield, quality, and adaptability in onion. Numerous studies have established that hybrid combinations consistently outperform their parental lines and open-pollinated varieties with respect to bulb yield, earliness, uniformity, and stress tolerance (Jones and Clarke, 1943; Hosfield et al., 1977b; Madalageri, 1983). However, the practical exploitation of heterosis in onion was historically constrained by the crop's floral morphology, which makes manual emasculation technically difficult and economically unfeasible. The discovery of cytoplasmic male sterility (CMS) in onion by Jones and Clarke (1943) represented a major breakthrough, providing a practical and efficient mechanism for large-scale hybrid seed production. CMS-based hybrid breeding has since become the foundation of commercial onion improvement worldwide, enabling the development of genetically uniform, high-yielding hybrids with enhanced disease tolerance and environmental adaptability (Suciu and Tempelman, 1979; Havey, 1993; Jones et al., 2010; Singh et al., 2018). In recent years, CMS-based heterosis breeding has gained increasing relevance in tropical and subtropical regions, particularly for addressing the productivity and stability challenges associated with rainy season cultivation. Given the increasing demand for reliable onion production under monsoon conditions, CMS-based hybrid breeding offers a promising and sustainable strategy for improving yield stability, bulb quality, and disease tolerance during the kharif season. Against this background, the present review synthesizes current knowledge on onion botany, breeding behavior, male sterility systems, and heterosis breeding, with a specific focus on the role of CMS-based hybrids in enhancing rainy-season productivity. By critically analyzing existing research and identifying key breeding priorities and knowledge gaps, this review aims to provide a comprehensive framework to guide future onion improvement programs and strengthen the resilience of kharif onion production systems.

Contribution of Onion Seasons to Total Production in India.

Despite contributing a smaller share to total production, kharif and late kharif onions are crucial for maintaining market supply during the lean period between rabi harvests. However, productivity during the rainy season remains low due to excess moisture, disease incidence, and lack of well-adapted hybrids, emphasizing the need for targeted breeding interventions.

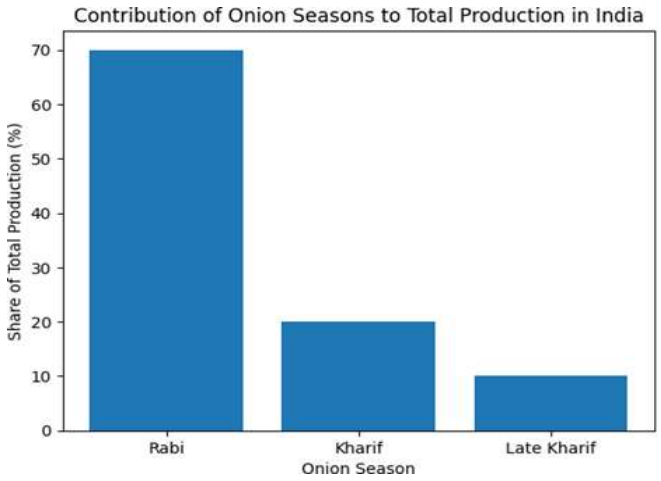


Figure 1. Relative contribution of rabi, kharif, and late kharif onion seasons to total onion production in India.

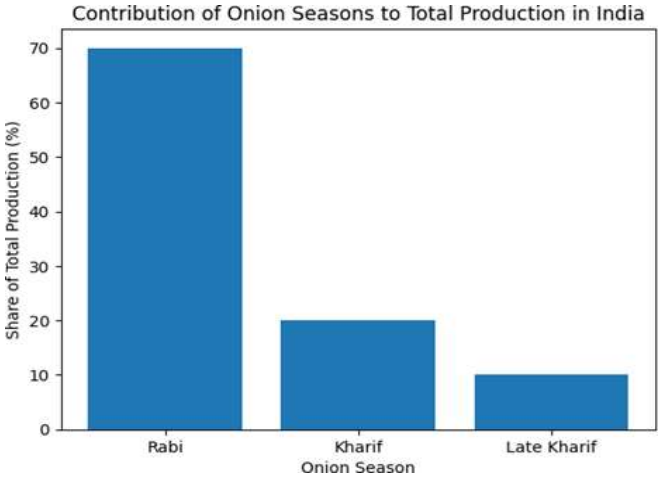


Figure 2. Major onion-growing states contributing to the kharif onion area in India.

2. Botany and Breeding Behavior of Onion (Allium cepa L.)

Onion (Allium cepa L.) belongs to the family Amaryllidaceae and the genus Allium, which comprises several economically important species such as garlic (A. sativum), leek (A. porrum), and shallot (A. cepa var. aggregatum). Allium cepa is a diploid species with a somatic chromosome number of 2n = 16 (Jones and Clarke, 1943). The crop exhibits a biennial life cycle, completing vegetative growth and bulb formation during the first year, followed by flowering and seed production in the second year after exposure to adequate vernalization and favorable photoperiod conditions (Jones and Davis, 1944; Piper, 1966). The reproductive biology of onion is characterized by umbel-type inflorescences bearing 50–100 small, perfect flowers. Flowering is typically protogynous, with stigma receptivity preceding pollen dehiscence, thereby promoting cross-pollination. Pollination is predominantly entomophilous, mediated by honeybees (Apis spp.) and various fly species, which facilitate extensive pollen flow within and among populations (Hosfield et al., 1976; Veere Gowda, 1988). This pollination mechanism results in a high degree of outcrossing, leading to substantial genetic variability and heterozygosity within onion populations. High heterozygosity is a defining feature of cultivated onion and has profound implications for its breeding behavior. While genetic variability provides opportunities for selection and heterosis exploitation, it also poses challenges for the

development of uniform inbred lines. Early studies demonstrated that repeated selfing or sib-mating leads to severe inbreeding depression, manifested as reduced vigor, poor bulb development, delayed maturity, and diminished seed set (Jones and Davis, 1944; Veere Gowda, 1988). As a consequence, the maintenance of highly homozygous and agronomically stable inbred lines in onion is both time-consuming and technically demanding. From a quantitative genetic perspective, many economically important traits in onion, including bulb yield, bulb size, shape, uniformity, and several quality attributes such as total soluble solids (TSS), dry matter content, and storage life, are governed predominantly by non-additive gene action (Hosfield et al., 1977a; Fraga et al., 2001; Kumar et al., 2015). Diallel and line × tester analyses have consistently revealed the preponderance of specific combining ability (SCA) effects over general combining ability (GCA) for yield and yield-related traits, indicating the importance of dominance and epistatic interactions. This genetic architecture strongly favors the exploitation of heterosis through hybrid breeding rather than improvement through conventional selection in open-pollinated populations. The biennial nature of onion further complicates breeding efforts by extending the breeding cycle and slowing genetic gain. Each generation requires two growing seasons—one for bulb production and another for seed multiplication making rapid recycling of generations difficult under conventional breeding schemes. Moreover, phenotypic expression of key traits such as bulb size, maturity, and storability is strongly influenced by environmental factors, including photoperiod, temperature, and soil moisture, which adds another layer of complexity to selection and evaluation. Taken together, the biological and genetic characteristics of onion namely its cross-pollinated breeding system, high heterozygosity, pronounced inbreeding depression, predominance of non-additive gene action, and extended breeding cycle clearly indicate the limitations of conventional pure-line breeding approaches. Conversely, these same attributes make onion particularly well-suited for heterosis breeding. The ability to capture and stabilize hybrid vigor through the use of male sterility systems, especially cytoplasmic male sterility (CMS), has therefore become central to modern onion improvement strategies. Understanding the botany and breeding behavior of onion provides the biological foundation for exploiting CMS-based heterosis breeding. The following sections examine the genetic and mechanistic basis of male sterility in onion, its classification, and its strategic application in commercial hybrid development, with particular emphasis on improving yield stability and quality under challenging rainy season cultivation conditions.



Figure 1: Botany and Breeding Behavior of Onion (Allium cepa L.)

3. Male Sterility in Onion: Concepts, Classification, and Genetic Control

Male sterility is a naturally occurring reproductive phenomenon in flowering plants and has assumed major importance in modern plant breeding, particularly for the development of hybrid cultivars. In crops such as onion (Allium cepa L.), where flowers are small, numerous, and arranged in umbels, manual emasculation is technically difficult, labor-intensive, and economically unfeasible. Under such circumstances, male sterility provides an efficient biological mechanism for preventing self-pollination and facilitating controlled cross-pollination, thereby enabling large-scale hybrid seed production (Jones and Clarke, 1943; Jones and Davis, 1944; Jones et al., 2010). Male sterility is defined as the inability of a plant to produce functional pollen due to the absence of viable stamens or the development of malformed or non-dehiscent anthers, while the female reproductive organs remain fully functional. Although male-sterile individuals are generally eliminated under natural selection, the trait has been deliberately conserved and exploited in cultivated crops because of its immense value in hybrid breeding programs (Vavilov, 1951; Hallauer and Miranda, 1982). In onion, male sterility functions as a natural system of genetic emasculation, allowing efficient and reliable exploitation of heterosis without the need for mechanical or chemical emasculation.

3.1 Classification of Male Sterility in Onion

Based on the genetic and cytoplasmic factors governing its expression, male sterility in onion can be broadly classified into three categories:

1. Genic (Nuclear) Male Sterility (GMS)
2. Cytoplasmic Male Sterility (CMS)
3. Cytoplasmic–Genic Male Sterility (CGMS)

Each system differs in inheritance pattern, stability, and practical utility in hybrid breeding.

3.2 Genic (Nuclear) Male Sterility

Genic or nuclear male sterility is controlled exclusively by nuclear genes and follows Mendelian inheritance. Sterility may be governed by either recessive or dominant alleles, depending on the genetic system involved (Kempthorne, 1957; Falconer, 1981). Although GMS has theoretical value for hybrid development, its practical application in onion breeding is limited. Maintenance of male-sterile lines requires continuous identification and removal of fertile segregants, making large-scale seed production inefficient and costly. Consequently, GMS has not been widely adopted in commercial onion hybrid programs (Jones et al., 2010).

3.3 Cytoplasmic Male Sterility (CMS)

Cytoplasmic male sterility is maternally inherited and governed by factors located in the mitochondrial genome. CMS systems are characterized by stable transmission of male sterility through the female parent, making them inherently attractive for hybrid seed production (Jones and Clarke, 1943; Singh et al., 2018). However, CMS expression alone is often insufficient for breeding purposes unless it is complemented by appropriate nuclear gene interactions that allow maintenance and fertility restoration in hybrids.

3.4 Cytoplasmic–Genic Male Sterility (CGMS)

The most widely exploited and commercially successful system in onion is cytoplasmic–genic male sterility (CGMS), in which male sterility results from the interaction between sterile cytoplasm and specific nuclear genes. In this system, the expression of sterility or fertility is determined jointly by the type of cytoplasm and the allelic constitution at nuclear fertility restoration loci (Jones and Clarke, 1943; Jones et al., 2010). In onion, several sterile cytoplasms have been identified, including CMS-S, CMS-T, and CMS-R, each differing in stability and breeding utility. Among these, CMS-S is the most extensively studied and widely utilized in hybrid breeding programs because of its high stability and the availability of effective maintainer lines (Jones and Clarke, 1943; Singh et al., 2018). Other cytoplasms, such as CMS-T, have shown environmental sensitivity and limited commercial application.

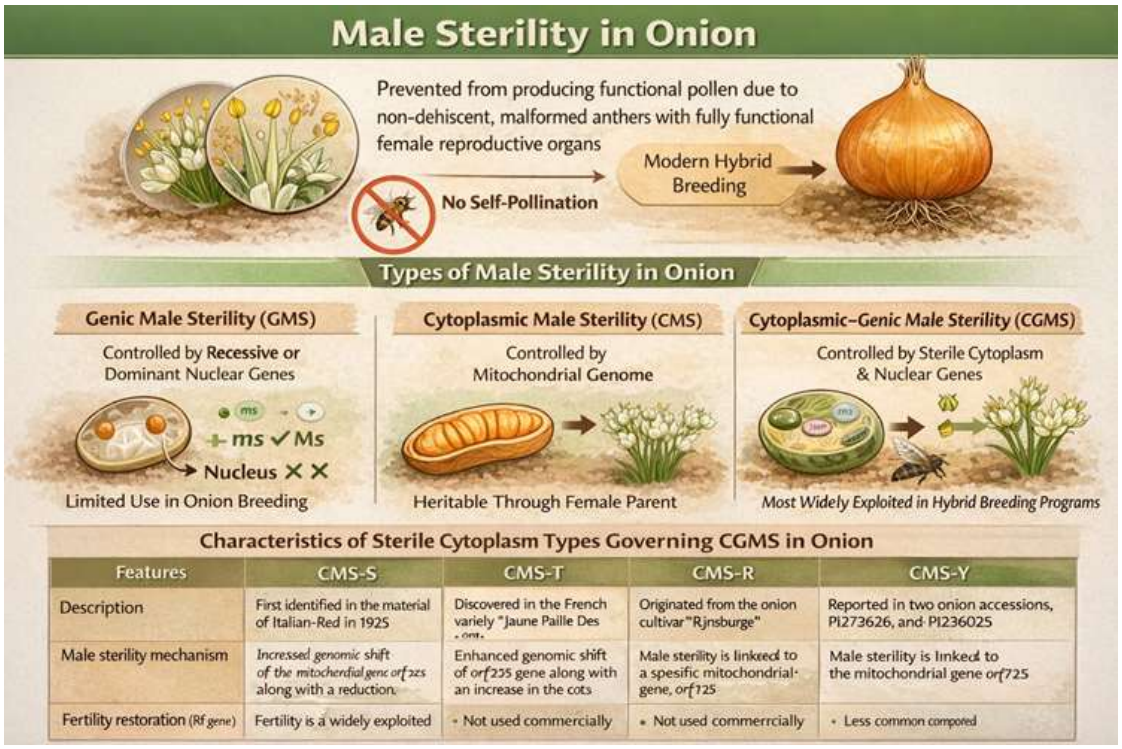


Figure 2: Male Sterility in Onion

3.5 Genetic Control of CGMS in Onion

The first report of male sterility in onion was made by Jones (1925) in the cultivar 'Italian Red,' and the genetic basis of this phenomenon was subsequently elucidated by Jones and Clarke (1943). They demonstrated that male sterility in onion is associated with sterile cytoplasm (S) interacting with recessive nuclear alleles at the male sterility locus (ms). In this CGMS system, plants possessing sterile cytoplasm (S) and homozygous recessive nuclear genotype (msms) express complete male sterility. In contrast, plants carrying one or two dominant nuclear alleles (Ms) remain fertile irrespective of cytoplasmic type.

The nuclear male sterility gene in diploid onion occurs in three genotypic forms:

- MsMs: dominant homozygous, fertile
- Msms: heterozygous, fertile
- msms: recessive homozygous, male sterile in S cytoplasm

These nuclear genotypes can occur in association with either sterile (S) or normal (N) cytoplasm, and the interaction between cytoplasmic type and nuclear genotype determines the final phenotypic expression of fertility or sterility (Jones and Clarke, 1943; Jones and Davis, 1944).

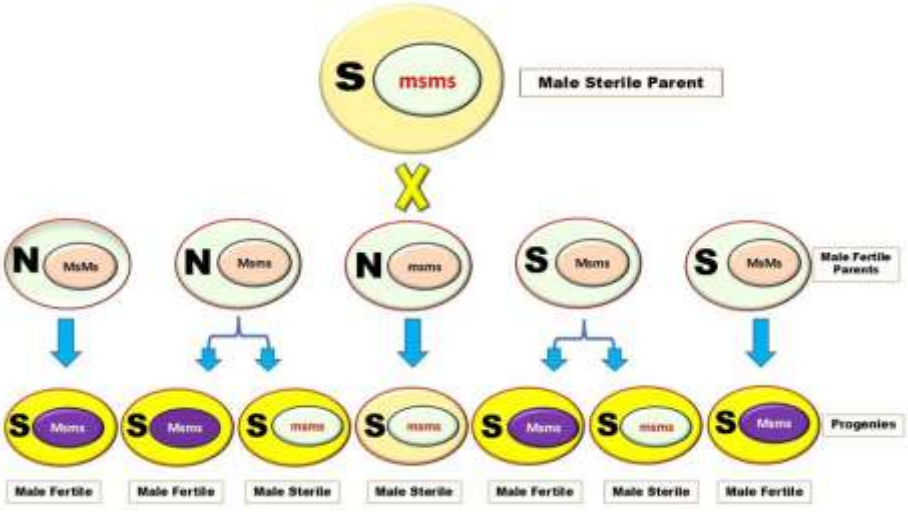


Figure 3:

3.6 Maintenance and Utilization of Male-Sterile Lines

Stable maintenance of male-sterile lines is achieved through the use of corresponding maintainer lines. Male-sterile A-lines possessing sterile cytoplasm and recessive nuclear genotype (S msms) are maintained by crossing them with genetically identical B-lines carrying normal cytoplasm but the same recessive nuclear genotype (N msms). This A/B line system ensures reliable perpetuation of male sterility across generations (Jones and Clarke, 1943; Singh et al., 2018). Hybrid seed production is accomplished by crossing the male-sterile A-line with a fertile restorer (R-line) carrying dominant fertility-restoring allele(s). The resulting F_1 hybrids are fertile and express heterosis for yield, quality, and adaptability. This three-line CGMS system forms the backbone of commercial onion hybrid breeding worldwide (Jones et al., 2010). The CGMS system has been extensively exploited for the development of high-yielding onion hybrids with improved bulb size, uniformity, quality traits, disease resistance, and wide adaptability across diverse agro-climatic environments (Suciu and Tempelman, 1979; Kumar et al., 2015; Singh et al., 2018; Veere Gowda and Ambresh, 2014). Its reliability, scalability, and compatibility with modern breeding tools make CGMS the most effective mechanism for harnessing heterosis in onion.

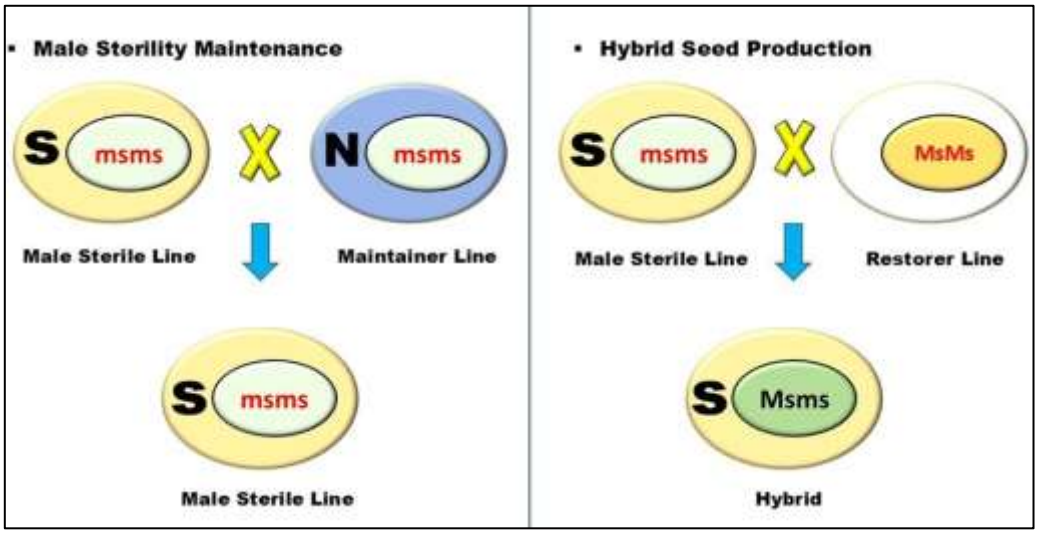


Figure 4: Maintenance and Utilization of Male-Sterile Lines

4. Heterosis Breeding in Onion (Allium cepa L.)

Enhancing crop productivity through genetic improvement remains a central objective of modern plant breeding, and the exploitation of heterosis or hybrid vigor has proven to be one of the most effective strategies for achieving this goal. Heterosis breeding has transformed yield improvement programs in both self- and cross-pollinated crops (Shull, 1908; Falconer & Mackay, 1996). In onion (Allium cepa L.), a naturally cross-pollinated and highly heterozygous species, heterosis breeding offers exceptional potential for improving yield, bulb quality, and environmental adaptability (Havey, 1993; Singh et al., 2019). Onion is among the few vegetable crops in which heterosis has been successfully exploited on a commercial scale for several decades, particularly in countries with advanced seed industries. Hybrid onion cultivars have consistently demonstrated superiority over open-pollinated varieties with respect to total bulb yield, earliness, bulb size and uniformity, shelf life, and resistance or tolerance to major diseases (Jones & Clarke, 1943; Brewster, 2008; Pathak et al., 2014). Despite India's position as one of the largest onion producers globally, systematic heterosis breeding, especially in the public sector, received limited attention until relatively recently, resulting in a slower pace of hybrid development tailored to local agro-climatic conditions (Singh et al., 2018; Khar et al., 2022). Globally, onion cultivation continues to rely predominantly on open-pollinated varieties, while commercial hybrids are largely confined to long-day types grown in temperate regions such as the United States, Europe, and Japan (Brewster, 2008; Havey & Bark, 2010). In contrast, onion production in tropical and subtropical regions, including the Indian subcontinent, depends primarily on short-day cultivars. Consequently, the development of short-day

onion hybrids adapted to tropical environments is a critical prerequisite for improving productivity in these regions (Kumar et al., 2017; Singh et al., 2020). The integration of cytoplasmic male sterility (CMS) systems into breeding programs has played a pivotal role in enabling cost-effective hybrid seed production and ensuring genetic uniformity in hybrid progeny (Jones & Clarke, 1943; Evoor et al., 2007; Havey, 2013). Until the past decade, most commercially available onion hybrids in India were developed and marketed by private seed companies, often with limited adaptation to region-specific production constraints. More recently, public-sector institutions, including ICAR institutes and State Agricultural Universities, have initiated CMS-based hybrid breeding programs aimed at developing short-day onion hybrids specifically adapted to Indian agro-ecologies (Khar et al., 2011; Singh et al., 2019). These efforts are particularly relevant for the North Indian plains and central Indian regions, where photoperiod sensitivity, temperature regimes, and disease pressure differ markedly from those in temperate environments (Tripathy et al., 2013; Pathak et al., 2019).

4.1 Genetic Basis of Heterosis in Onion

Extensive genetic studies have elucidated the genetic basis underlying heterosis expression in onion. Diallel and line × tester analyses have consistently revealed the predominance of non-additive gene action for bulb yield and many associated traits, including bulb size, diameter, and uniformity (Hosfield et al., 1977a; Hosfield et al., 1977b; Madalageri, 1983; Veere Gowda, 1988). High specific combining ability (SCA) effects relative to general combining ability (GCA) effects indicate the importance of dominance and epistatic interactions in governing these traits. The strong influence of non-additive gene action provides a robust genetic justification for heterosis breeding in onion. It also explains the limited success of conventional selection approaches in improving complex quantitative traits such as yield and yield stability. By capturing favorable allelic interactions through hybridization, CMS-based hybrids effectively translate genetic potential into superior field performance.

4.2 Magnitude and Consistency of Heterosis

Numerous studies have documented substantial and consistent heterosis for economically important traits in onion. Reported heterosis for bulb yield typically ranges from 30% to 60% over the better parent, with significant improvements also observed for average bulb weight, bulb diameter, and marketable yield (Fraga et al., 2001; Borgaonkar et al., 2005; Kumar et al., 2015). Positive heterotic effects have also been reported for earliness, with hybrids maturing 10–25% earlier than their parental lines, enabling better escape from late-season disease pressure and adverse weather conditions (Joshi and Tanodom, 1976; Abubakar and Ado, 2008). Beyond yield, heterosis in onion extends to several quality traits. Hybrid cultivars often exhibit higher total soluble solids (TSS), improved dry matter content, enhanced bulb uniformity, and superior storage life compared with open-pollinated varieties (Pal et al., 1988; Hayes and Randle, 1996; Kumar et al., 2015). These attributes are particularly valuable in commercial onion production, where uniformity, storability, and processing suitability directly influence market value and profitability.

4.3 Heterosis Breeding under Rainy Season Conditions

The advantages of heterosis breeding are especially pronounced under suboptimal and stress-prone environments, such as rainy (kharif) season cultivation. CMS-based onion hybrids have consistently demonstrated greater yield stability, improved tolerance to biotic stresses, and enhanced adaptability under conditions of high humidity, intermittent waterlogging, and severe disease pressure. Hybrids often display more vigorous vegetative growth, uniform bulbing, and synchronized maturity, traits that contribute to improved harvest efficiency and marketable yield during the rainy season. Cytoplasmic male sterility (CMS)-based hybrid breeding has become a key strategy in onion (Allium cepa L.) improvement, enabling efficient F_1 hybrid seed production and exploitation of heterosis for agronomic traits including stress tolerance and disease resistance. Several studies have reported that CMS-derived onion hybrids exhibit reduced disease severity for important fungal pathogens compared with non-hybrid or open-pollinated cultivars, contributing to improved crop resilience. Notably, CMS-based hybrids have been

associated with lower anthracnose severity caused by Colletotrichum spp. in onion production systems, a disease complex that causes foliar lesions, neck rot and bulb losses. In addition, hybrid performance under Fusarium basal rot (FBR) pressure, caused by Fusarium oxysporum f. sp. cepae, has also been favorably documented, with lower disease incidence and severity observed in heterotic cultivars developed using CMS systems. These findings suggest that integrating CMS lines with favorable parental sources of resistance can lead to hybrids with quantitatively reduced disease severity for both anthracnose and basal rot, supporting sustainable disease management in onion production. These findings underscore the potential of heterosis breeding as a practical strategy for stabilizing onion production during the kharif season, when conventional varieties frequently fail to perform reliably.

4.4 Progress and Limitations in Onion Heterosis Breeding

Despite significant progress, heterosis breeding in onion faces several constraints. The narrow genetic base of available CMS lines and fertility restorers, environmental sensitivity of sterility expression in some cytoplasmic systems, and challenges associated with hybrid seed production remain important limitations. Additionally, genotype × environment interactions can influence heterosis expression, necessitating extensive multi-location evaluation to identify broadly adapted hybrid combinations. Recent advances in breeding technologies offer promising solutions to these challenges. The development of doubled haploid lines has accelerated the production of homozygous parental lines, while molecular markers linked to CMS cytoplasms and fertility restoration genes have improved the efficiency and precision of parental line development. Integration of these tools with conventional breeding approaches has the potential to significantly enhance the effectiveness of heterosis breeding programs in onion.

Table 1. Major milestones in heterosis and CMS-based hybrid breeding in onion

Year	Key finding / contribution	Reference
1943	Discovery of cytoplasmic male sterility (CMS) and its inheritance in onion	Jones & Clarke (1943)
1944	Demonstration of inbreeding depression and heterosis in onion	Jones & Davis (1944)
1976–77	Evidence of significant heterosis and combining ability through diallel analysis	Hosfield et al. (1976, 1977a, 1977b)
1983–88	Confirmation of predominance of non-additive gene action for yield traits	Madalageri (1983); Veere Gowda (1988)
1988	Heterosis reported for yield, storage and dehydration quality	Pal et al. (1988)
2001–05	Large magnitude of heterosis for bulb yield reported in hybrids	Fraga et al. (2001); Borgaonkar et al. (2005)
2002 onwards	Development and use of doubled haploid lines in onion	Bohanec (2002); Kim et al. (2007)

Table 2. Magnitude of heterosis reported for yield and yield-related traits in onion

Trait	Reported heterosis (%)	Key references
Bulb yield	30–60% over better parent	Fraga et al. (2001); Borgaonkar et al. (2005); Kumar et al. (2015)
Average bulb weight	20–45%	Hosfield et al. (1977b); Evoor et al. (2007)
Earliness	10–25%	Joshi & Tanodom (1976); Abubakar & Ado (2008)
Bulb diameter	15–40%	Aghora (1985); Divakar (2001)
Yield stability	High across environments	Quartiero et al. (2014)

Table 3. Heterosis for quality traits in onion hybrids

Quality trait	Improvement through heterosis	References
Total soluble solids (TSS)	Increased TSS and dry matter	McCollum (1968); Hayes & Randle (1996)
Pungency	Moderate improvement with stability	Pal et al. (1988)
Storage life	Improved shelf life and reduced rotting	Pal et al. (1988); Kumar et al. (2015)
Bulb uniformity	Highly uniform bulbs	Hosfield et al. (1977a)
Processing suitability	Better dehydration quality	Pal et al. (1988)

Table 4. CMS systems in onion and their breeding significance

CMS type	Stability	Use in breeding	Remarks	References
S-cytoplasm	High	Widely used	Stable sterility and good maintainers available	Jones & Clarke (1943); Jones et al. (2010)
T-cytoplasm	Moderate	Limited use	Environmental sensitivity reported	Jones et al. (2010)

5. Advantages of CMS-Based Hybrids for Rainy Season Onion Cultivation

Onion (Allium cepa L.) is a highly cross-pollinated crop that exhibits pronounced inbreeding depression, resulting in poor field performance of inbred lines under commercial cultivation. Consequently, hybrid breeding that exploits heterosis represents the most effective approach for achieving higher and more stable yields, improved bulb uniformity, and enhanced adaptation to adverse environments such as rainy (kharif) season cultivation. However, the practical implementation of hybrid breeding in onion is severely constrained by the crop's small flower size and umbel inflorescence, which render manual emasculation technically difficult, labour-intensive, and economically impractical. Under these conditions, male sterility systems provide a biologically efficient and commercially viable alternative for large-scale hybrid seed production (Havey, 2000; Singh et al., 2013). Among the different male sterility systems identified in onion, cytoplasmic–genic male sterility (CGMS) has been the most widely and successfully exploited in commercial hybrid development. The S-cytoplasm (CMS-S), first identified in the onion line 'Italian Red 13-53', remains the most extensively utilized cytoplasm due to its high stability and the availability of effective maintainer lines. In this system, male sterility results from the interaction between mitochondrially encoded sterile cytoplasm and recessive nuclear alleles at the Ms locus, leading to complete pollen sterility in the absence of dominant fertility-restoring alleles (Jones and Clarke, 1943; Havey, 1993; Havey, 2000). Hybrid seed production in onion typically follows a three-line breeding system consisting of a male-sterile A-line (sterile cytoplasm), a fertile maintainer B-line (normal cytoplasm with identical nuclear background), and a fertility restorer R-line carrying dominant restorer allele(s). Controlled crosses between the A-line and R-line result in fertile F_1 hybrids that express high levels of heterosis for yield, bulb quality, and stress tolerance (Singh et al., 2013; Khar et al., 2015). This system ensures genetic uniformity, scalability of seed production, and reliable expression of hybrid vigor. CMS-based onion hybrids have consistently demonstrated superior agronomic performance compared with open-pollinated varieties. These advantages include enhanced vegetative vigor, uniform bulb size and shape, higher marketable yield, improved bulb skin quality, and superior storage life. Such traits are particularly critical under rainy season cultivation, where high humidity, intermittent waterlogging, and disease pressure demand greater physiological robustness and uniformity for stable production (Lawande et al., 2019). One of the most significant advantages of CMS-based hybrids under kharif conditions is improved tolerance to biotic stresses. Several studies have reported reduced severity of major foliar diseases such as anthracnose (Colletotrichum spp) and Fusarium basal rot (Fusarium oxysporum f. sp. cepae) in CMS-derived hybrids, likely due to enhanced plant vigor and favorable gene interactions expressed through heterosis (Abubakar and Ado, 2008; Veere Gowda

and Ambresh, 2014). Improved disease tolerance directly contributes to higher marketable yield and reduced dependence on chemical control measures, thereby lowering production costs and environmental impact. CMS-based hybrids also offer greater yield stability across environments, a trait of paramount importance under the highly variable climatic conditions of the monsoon season. Uniform bulbing, synchronized maturity, and improved partitioning of assimilates in hybrids facilitate timely harvesting and reduce losses associated with uneven maturity and disease incidence. Furthermore, early-maturing hybrids enable partial escape from late-season disease outbreaks and unfavorable weather conditions, enhancing overall production reliability. Recent advances in molecular genetics and genomics have further strengthened CMS-based onion breeding. Molecular markers have been developed for reliable identification of different cytoplasm types (S, T, N, R) and for detecting fertility restoration alleles at the Ms locus. Marker-assisted selection has significantly improved the efficiency of parental line development, reduced breeding cycle duration, and enhanced the precision of hybrid breeding programs (Havey and Wolff, 2012; Kim et al., 2019; Khar et al., 2020). These tools are particularly valuable for accelerating the development of region-specific hybrids adapted to rainy season cultivation. Collectively, the advantages of CMS-based hybrids ranging from enhanced yield and quality to improved disease tolerance and yield stability underscore their critical role in strengthening onion production systems under challenging monsoon environments. Their continued refinement and deployment are essential for ensuring sustainable and profitable onion cultivation during the rainy season.

6. Breeding Priorities and Research Focus for Kharif Onion Hybrids

The successful development and large-scale adoption of onion hybrids for rainy (kharif) season cultivation require a strategic realignment of breeding priorities to address the unique agro-climatic and biotic challenges associated with monsoon environments. Unlike rabi-grown onion, kharif onion is exposed to high humidity, erratic rainfall, elevated temperatures during early growth stages, and intense disease pressure, all of which necessitate targeted breeding interventions. CMS-based heterosis breeding provides a robust platform for meeting these challenges, but its effectiveness depends on the careful identification and integration of priority traits into hybrid development pipelines.

6.1 Yield Stability and Environmental Adaptation

Yield stability across variable environments is the foremost breeding priority for kharif onion hybrids. Strong genotype × environment interactions frequently limit the performance of otherwise high-yielding genotypes under monsoon conditions. Therefore, breeding programs must emphasize the selection of parental lines and hybrid combinations that exhibit consistent performance across locations and seasons. CMS-based hybrids with enhanced buffering capacity against abiotic stresses particularly excess soil moisture, transient waterlogging, and temperature fluctuations are critical for stabilizing onion production during the rainy season. Multi-location and multi-season evaluation of experimental hybrids should be an integral component of kharif onion breeding programs to identify broadly adapted genotypes. The integration of physiological traits such as root system architecture, efficient nutrient uptake under saturated soils, and robust canopy structure may further enhance environmental adaptability and yield stability.

6.2 Disease Resistance and Tolerance

Biotic stress tolerance represents a major breeding objective for rainy-season onion cultivation. High humidity and prolonged leaf wetness during the monsoon create ideal conditions for the development of foliar diseases such as anthracnose (Colletotrichum spp) and Fusarium basal rot (Fusarium oxysporum f. sp. cepae). Breeding for durable resistance or tolerance to these diseases is essential for minimizing yield losses and reducing reliance on fungicidal sprays. Given the limited availability of strong single-gene resistance sources in onion, breeding efforts should prioritize quantitative and polygenic resistance mechanisms. CMS-based hybrids can effectively combine complementary resistance alleles from diverse parental backgrounds, thereby enhancing overall disease tolerance through heterosis. Screening under natural epiphytotic conditions, combined with controlled inoculation assays, will improve the reliability of resistance evaluation.



Figure 5: Symptoms sequence of onion anthracnose & fusarium basal rot (FBR)

6.3 Bulb Quality and Market Acceptability

Bulb quality traits remain critical determinants of market value and consumer preference, particularly under kharif cultivation where environmental stress often compromises bulb uniformity and storability. Breeding priorities should include the development of hybrids with uniform bulb size and shape, strong and well-adhered bulb skins, and acceptable pungency levels. Improved bulb skin integrity is especially important under rainy conditions, as it reduces susceptibility to post-harvest diseases and mechanical damage during handling and transport. Dry matter content and total soluble solids (TSS) are also important quality parameters, influencing both culinary value and processing suitability. CMS-based hybrids frequently exhibit favorable heterotic responses for these traits, and their consistent expression should be emphasized during hybrid evaluation.

6.4 Earliness and Crop Duration

Earliness is a strategically important trait for kharif onion hybrids, as it enables partial escape from late-season disease outbreaks and adverse weather conditions. Early-maturing hybrids allow timely harvesting before peak monsoon intensity, thereby reducing field losses and improving bulb quality. Short-duration hybrids also facilitate better cropping system integration, enabling farmers to fit onion into intensive and diversified production schedules. Breeding programs should target the development of hybrids that combine early maturity with adequate bulb size and yield potential. This balance is essential to ensure that earliness does not come at the expense of marketable yield.

6.5 Strengthening CMS and Restorer Line Resources

The long-term success of CMS-based heterosis breeding depends on the availability of diverse and stable male-sterile (A) lines and effective fertility restorer (R) lines. Many existing onion hybrids rely on a narrow genetic base of CMS sources, increasing the risk of vulnerability to biotic and abiotic stresses. Expanding the cytoplasmic and nuclear diversity of CMS and restorer lines is therefore a key research priority. Systematic identification of new maintainer and restorer lines, combined with regular monitoring of sterility stability under different environmental conditions, is essential. Molecular markers linked to cytoplasm types and fertility restoration genes should be routinely integrated into breeding programs to improve selection efficiency and reduce the time required for parental line development.

6.6 Integration of Modern Breeding Tools

The incorporation of modern breeding tools has the potential to significantly accelerate the development of superior kharif onion hybrids. Marker-assisted selection (MAS) can facilitate the rapid identification of CMS cytoplasms, restorers, and disease-tolerant genotypes, while genomic selection offers opportunities to improve complex traits such as yield stability and stress tolerance. Advances in doubled haploid technology, although still challenging in onion, provide promising avenues for the rapid

development of homozygous parental lines. Additionally, high-throughput phenotyping and environmental characterization can enhance the precision of selection under variable monsoon conditions.

CONCLUSIONS AND FUTURE PERSPECTIVES

Onion (Allium cepa L.) is a crop of substantial economic and nutritional importance, yet its productivity particularly during rainy (kharif) season cultivation remains constrained by complex interactions among environmental stresses, disease pressure, and inherent biological limitations. The cross-pollinated nature of onion, high heterozygosity, pronounced inbreeding depression, and predominance of non-additive gene action collectively limit the effectiveness of conventional selection-based breeding approaches. In this context, CMS-based heterosis breeding has emerged as the most efficient and sustainable strategy for achieving significant genetic gains in yield, quality, and adaptability. This review highlights that the successful exploitation of heterosis in onion has been largely enabled by stable cytoplasmic–genic male sterility systems, particularly the S-cytoplasm, which allow economical and reliable hybrid seed production. CMS-based hybrids consistently outperform open-pollinated varieties in terms of bulb yield, uniformity, storability, and yield stability, with these advantages being especially pronounced under the stress-prone conditions of rainy season cultivation. Enhanced tolerance to major foliar diseases, synchronized maturity, and improved physiological vigor further strengthen the suitability of hybrids for monsoon environments. Despite these advances, several challenges continue to constrain the full realization of hybrid breeding potential in onion. The narrow genetic base of CMS sources and fertility restorers, environmental sensitivity of sterility expression in certain cytoplasmic systems, and limited availability of well-characterized disease resistance sources remain key bottlenecks. Addressing these constraints requires sustained efforts to diversify CMS and restorer line resources, strengthen pre-breeding programs, and systematically evaluate hybrids across diverse environments to ensure broad adaptation and stability. Looking ahead, the integration of modern breeding tools with conventional CMS-based breeding strategies offers significant opportunities for accelerating progress. Marker-assisted selection for cytoplasm type, fertility restoration, and disease tolerance, coupled with genomic selection for complex traits such as yield stability and stress resilience, can substantially enhance breeding efficiency. Advances in doubled haploid technology, high-throughput phenotyping, and precise environmental characterization are expected to further shorten breeding cycles and improve selection accuracy. From a practical perspective, the development of region-specific, early-maturing, and disease-tolerant kharif onion hybrids should be prioritized to stabilize production, reduce crop losses, and enhance farmer profitability. Strengthening public–private partnerships, improving hybrid seed production infrastructure, and facilitating wider dissemination of adapted hybrids will be critical for translating breeding advances into tangible gains at the farm level. In conclusion, CMS-based heterosis breeding represents a cornerstone of modern onion improvement, particularly for overcoming the challenges associated with rainy season cultivation. Continued innovation, genetic diversification, and strategic integration of emerging technologies will be essential for ensuring sustainable onion productivity and resilience in the face of increasing climatic variability.

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