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Cytoplasmic Male Sterility in Pearl Millet [*Pennisetum americanum* (L.) Leeke]—A Review*

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I. Introduction

Pearl millet [*Pennisetum americanum* (L.) Leeke] is a staple food for millions of people in several African countries and in the Indian subcontinent. It is grown on an estimated 26 million ha in these two regions with an annual production of about 13 million metric tons (Food

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and Agriculture Organization, 1978). The average grain yields of traditional cultivars (open-pollinated landrace varieties) are between 400 and 550 kg/ha.

In 1962, seed of the first cytoplasmic-genic male-sterile [or cytoplasmic male sterility (CMS), as it is normally termed] line of pearl millet developed in the United States was used by breeders in India to identify, and 3 years later to release, the first successful commercial grain hybrid. The floral biology and the resulting mating system facilitates the production of F_1 hybrids in this wind-pollinated crop (Burton and Powell, 1968; Duvick, 1966).

The history of development of CMS in pearl millet, and the foreseen need for it, has involved many scientists in two continents. While the application of CMS to crop production in India has been a success story, it has been beset by epidemics of downy mildew on successive hybrids, which remain a continuing threat. Cytoplasmic male sterility remains to be utilized in Africa, where the largest amount of pearl millet is grown in a wide range of diverse environments. There are regions, however, where, through the breeding of adapted seed parents, CMS has the potential to increase food production.

It is the purpose of this article to trace the discovery and use of CMS in pearl millet, but before reviewing the subject a description of the characteristics of flowering, the basis for cytoplasmic male sterility, and a summary of early breeding work are given.

A. CHARACTERISTICS OF FLOWERING

Pearl millet is protogynous; that is, the stylar branches are exerted from the florets 1 to several days before the anthers. Spikelets generally consist of two florets: one perfect and the other staminate. Stylar branches are usually first exerted from the florets in the upper half of the head, and by the third day nearly all styles will have emerged on the head. Generally, anthers emerge from the same florets that exerted styles first, beginning at least 1 day after complete stylar emergence. A head will normally shed pollen 4 to 6 days after first style emergence. A second flush of anthers may then emerge if the staminate florets are functional. Stigmas will remain receptive if not pollinated for up to 10 days, depending on weather conditions. Fertilization occurs within a few hours after pollination, and the stylar branches wilt and dry usually 24 hr after pollination (Burton, 1980). Thus the mating system of pearl millet encourages, but does not enforce, cross-pollination. Cross-pollination is observed to be around 70 to 80%, but some self-pollination

occurs because tillers may flower in succession (Rao *et al.*, 1951; Burton, 1974).

B. BASIS FOR CYTOPLASMIC MALE STERILITY

Cytoplasmic male sterility in pearl millet, where anthers fail to dehisce and pollen may not be properly formed or may be empty, results from the interaction of a "sterile" cytoplasm (termed A cytoplasm) with homozygous recessive alleles of nuclear genes causing male sterility, e.g., ms_c ms_c (Burton and Athwal, 1967, 1968). Lines with such a constitution are termed A lines. When in "normal" (N) cytoplasm, the same recessive homozygote ms_c ms_c does not cause male sterility since its genetic effect is not expressed in normal cytoplasm. Lines with this constitution are called maintainers, or B lines, since, when they are used to pollinate A lines, the result will again be all male-sterile plants (hence male sterility has been maintained). Large quantities of seed that will give all male-sterile plants can be produced this way and this method forms the basis for commercial hybrid seed production. The presence of a dominant Ms_c allele will cause male fertility regardless of the type of cytoplasm. Lines of the constitution Ms_c Ms_c are termed restorers (R lines—as are all male or "pollen parents" of hybrids) because, when they are used to pollinate A lines, resulting plants will be ms_c Ms_c and will therefore have male fertility restored.

C. EARLY BREEDING WORK

In India two breeding approaches were used prior to 1965 to develop high-yielding and stable genotypes taking advantage of the mating system. These were, first, to develop improved open-pollinated varieties, and, second, to breed single-cross hybrids without the use of CMS.

Mass selection has been the principal method used in the development of varieties. A few improved strains have been evolved by pure-line selection, but owing to the predominantly cross-pollinated nature of this crop, the chances of obtaining superior varieties by this approach were poor. Individual plant selections in Akola Bajri led to the development of three improved cultivars, Nos. 37, 54, and 59 (Pandya *et al.*, 1955). Selections in the local populations were made on the basis of well-filled, compact, long panicles; high grain weight; and uniformity in ripening. In this manner several improved varieties were evolved from local materials, notably CO2, CO3, AKP1, AKP2, RSJ, RSK, Punjab type 55, and A1/3 (Ahluwalia and Vittal Rao, 1964;

Khan *et al.*, 1958; Utkhede, 1972). In addition to using indigenous variability, introductions from African material were also used in developing varieties; for example, Babapuri and Jamnagar giant in Gujarat, AF-3 in Maharashtra, Improved Ghana (renamed Pusa Moti) in Delhi, and S-530 (an outcross of an African introduction with local varieties in the Punjab) were developed and released for cultivation (Joshi *et al.*, 1961; Athwal and Rachie, 1963). These improved open-pollinated varieties had, however, a low yield potential, giving average yields of 900–1200 kg/ha, and could not be maintained because of extensive outcrossing with local landraces.

The second approach of producing hybrids (without the use of CMS) was started in India in the early 1940s (Rao *et al.*, 1951; Chavan *et al.*, 1955). In 1943, at the Millet Breeding Station in Coimbatore, India, 15 F_1 crosses were made between eight different types of pearl millet. Evaluations showed that three of these F_1 hybrids gave 16–163% more grain yield than did the best parents. Between 1944 and 1946 an additional 86 F_1 hybrids were evaluated, of which 34 were superior to the best parent. Between 1946 and 1950 a further 743 F_1 hybrids were tested, of which 25 gave yields significantly superior to both the best parent and the check CO.1. Of these, two hybrids, X.1 and X.2 were multiplied by planting the respective parents in rows and harvesting and mixing the seed from both the parental rows. In 21 trials conducted in nine districts on farmers' fields of the then Madras presidency during 1949 and 1950, hybrids X.1 and X.2 yielded 48 and 44 % more grain, respectively, over the local check and were released for cultivation (Rao *et al.*, 1951). Similar attempts were made in the former Bombay state (Chavan *et al.*, 1955).

The principal constraint in the development and seed production of a good hybrid was the lack of a practical and easy method to produce 100% hybrid seed. This fact was recognized in 1951 by Rao *et al.*, who emphasized that

> The method of large scale production of hybrid seeds for distribution is a problem demanding particular attention in this crop due to the peculiar floral mechanism of the plant. *Perhaps induction of male-sterility in female rows (similar to detasseling in maize) may assure complete cross pollination.* But attempts so far made to induce male-sterility have not been successful.

Other limitations were the narrow adaptability and limited superiority of hybrids over the local varieties (Athwal, 1966).

During the same time that breeders in India were trying to develop hybrids in this crop, Burton (1948), with studies that began in 1936, reported that maximum forage yields (the principal use of pearl millet in the United States) could be obtained from the F_1 hybrid of two lines possessing high combining ability. He realized that most forage crops—with their small perfect flowers, few seeds per flower, and high seedling rates—do not lend themselves to controlled hybridization on the extensive scale required for commerical hybrid production; consequently, the economical production of commercial F_1 hybrid seed was seen as a major obstacle. Results from his experiments, with mixtures of parent and hybrid millet seed containing 90, 80, 50, and 20% hybrid seed together with pure seed of the parents, indicated that the mean forage production of the 90, 80, and 50% hybrid mixtures over 6 years did not differ significantly from that of pure hybrids. The use of a high seed rate, with consequent natural elimination of the weaker parental seedlings or by selective thinning, increases the proportion of hybrid seedlings to be established, and over a period of years, any seed mixture within the range of 50–90% was expected to yield as much as pure hybrid seed (Burton, 1948).

Burton (1948) realized the importance of CMS for the commercial production of hybrids, as did the workers in India (Rao *et al.*, 1951). Burton detected self-sterility in many lines but commented that the *"difficulties associated with maintaining and using such lines in a commercial seed production program of an annual grass were so great as to make their use seem impractical."*

To circumvent the difficulty of providing pure hybrid seed to farmers, Athwal (1961) suggested the use of the xenia effect using a yellow seed color or some other marker gene for eliminating nonhybrid seed or seedlings.

To summarize, research during this period clearly indicated that large yield increases were possible with F_1 hybrids and that there was an absolute need for a system such as CMS to exploit heterosis on a commercial scale.

III. Cytoplasmic and Other Types of Male Sterility

A. Discovery and Development of CMS Lines

As early as 1940 Kadam *et al.* observed various forms of male sterility when inbreeding local millet from Nasik in the Bombay presidency, but did not conceive of the sterility as useful in hybrid production.

Kajjari and Patil (1956) reported the occurrence of spikes producing shriveled anthers without pollen in crossbred progenies. On bagging some of these spikes, no seed was obtained in those left unpollinated,

but those that were dusted with pollen from normal spikes set seed fully. These researchers suggested, but did not establish, that the observed male sterility could be of a cytoplasmic type and realized that it could be used to produce 100% hybrid seed.

Burton (1958) observed CMS in the winter of 1955–1956, in a cross designated 556 × 23, where 2 of the 4 selected F_2 plants failed to shed pollen or set seed when selfed. When these 2 male-sterile plants were again pollinated (backcrossed) by 23, the F_1 progeny again failed to shed pollen or to set seed when selfed. However, when pollen from other lines was used, seed set was complete, thus suggesting CMS. When a range of 41 inbreds were used as pollen parents on these male-sterile plants [(556 × 23) × 23], 6 of the resulting F_1 progeny were male sterile, 8 others were partially male sterile, and 27 were male fertile, proving conclusively that CMS in pearl millet had been found and at the same time showing that male fertility could easily be restored. Thus the first CMS line, Tift 23A, which was developed by repeated backcrossing with Tift 23B (maintainer), was released in 1965 (Burton, 1965a, 1969). Burton (1969) also developed dwarf versions of Tift 23A and B, called Tift 23DA and Tift 23DB, by transferring the recessive *d2* gene through a series of backcrosses into Tift 23A and Tift 23B. He also observed that since the tall and dwarf versions are near isogenic, similar heterogenic responses should be found in hybrid combinations. A dwarf male-sterile line such as 23DA with a tall male pollinator should produce more hybrid seed and should make better quality forage compared with tall sister hybrids (Burton, 1969).

Madhava Menon (1958), at the Millets Breeding Station, Coimbatore, observed in 1949 a high frequency of male-sterile plants showing underdeveloped, nondehiscent anthers in an open-pollinated population, PT819, originating from the Bellary district of Mysore state. No seed was set in selfed spikes of male-sterile plants, whereas in open-pollinated or artificially pollinated spikes, seed set was total, indicating normal female fertility. Two of seven crosses made with PT819 male-sterile plants in 1950 gave male-sterile F_1 hybrids, whereas the three testcrosses with male-fertile PT819 plants gave both male-sterile and male-fertile plants. The 2 male-sterile F_1 hybrids (PT819 × PT732/5 and PT819 × PT837/7) were backcrossed to the male parents (PT732/5 and PT837/7) using individual plants. Of the 22 hybrids evaluated, 13 were male-sterile, 2 were male-fertile, and 7 segregated in a 1:1 proportion for male-sterile and male-fertile plants. These results led Madhava Menon (1959) to conclude that "male-sterility observed in PT819 is dependent on an interaction between nuclear and cytoplasmic factors." Though this CMS source was found

and backcrossed again in 1951, unfortunately these lines were subsequently left out of further maintenance and were eventually lost (Appadurai and Sambathkumar, 1976). Work on new crosses of PT819 × PT732 reported by Appadurai *et al.* (1982) indicates that this CMS source may have been rediscovered and that it differs from several other male-sterile lines and their maintainers on which it was tested.

Athwal (1961) identified CMS in the late-maturing genetic stock IP189 (a selfed progeny of an African variety) at Ludhiana. The CMS plants were pollinated with pollen from different sources for maintenance and the line developed was designated as CMS 66A (also referred to as L66A). During 1962, male-sterile plants noticed in a segregating population from a natural cross (outcross) in a stock possessing pearly amber-colored grains were used to develop CMS 67A (L67A) (Athwal, 1966).

Burton (1965b) developed Tift 18A and Tift 18B inbreds by repeatedly backcrossing CMS Tift 23A with Tift 18, which carries a dormancy factor that inhibits premature germination.

Athwal (1966) reported the development of 11 new CMS lines at Ludhiana. These are L101, L102, L104, L105, L106, L107, L110, and L111, which incorporate Tift 23A sterile cytoplasm; L103 incorporates the sterile cytoplasm of L66A, and L108 and L109 incorporate the sterile cytoplasm of L67A. In each case sterile cytoplasm was introduced by repeated backcrossing into the identified maintainer starting in 1962. The distinguishing morphological characters of these CMS lines are described by Athwal *et al.* (1976).

In 1968, Burton and Athwal (1969) released a dwarf maintainer Tift 239DB (an inbred derived by introducing the *d2* dwarf gene into Tift 13) and its corresponding sterile Tift 239DA, which incorporates the sterile cytoplasm of L103A.

A number of other CMS lines have been developed since the late 1960s. D202A was developed at the Indian Agricultural Research Institute (IARI), New Delhi, in 1966, as a selection in the tall CMS line Tift 18B (Utkhede, 1972). Vohra (1969) isolated a dwarf CMS line designated as 18D2A from the tall Tift 18B at Jamnagar. Four CMS lines, 28A, 330A, 558A, and 628A, were developed at the Regional Research Center of IARI at Kanpur (Utkhede, 1972). Pokhriyal *et al.* (1976), at IARI, New Delhi, bred 5071A (an induced downy-mildew-resistant mutant from Tift 23B), 5054A (a Nigerian line, Kano 2457, incorporating sterile cytoplasm of Tift 23A), and 5141A (an inbred of Indian origin from Baroda 4, which also incorporates the sterile cytoplasm of Tift 23A). Gill *et al.* (1979), at Ludhiana, developed Pb 304A and Pb 405A as induced downy-mildew-resistant mutants from

Tift 239DB and L110B, respectively. Gill *et al.* (1981) reported the isolation of a natural downy-mildew-resistant mutant of Tift 23A—designated as Pb 204A—from a population of Tift 23A and Tift 23B. At the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) an induced downy-mildew-resistant mutant was isolated from an irradiated Tift 23DB population with rigorous screening at each selection and backcross generation in the downy mildew nursery (Williams *et al.*, 1981). This was designated as ICM ms81A and B and was distributed to research workers in 1981 (Andrews and Anand Kumar, 1982).

Burton (1981a,b) reported the development of Tift 23DAE and Tift 23DBE, which are early and photoperiod-insensitive versions of Tift 23DA and Tift 23DB. The early gene was transferred by repeated backcrossing from a weak, spindly, very early-maturing plant discovered in a field of "Katherine" pearl millet growing in Queensland, Australia. Powell and Burton (1973) introduced a recessive trichomeless gene (*tr*) into the normally pubescent Tift 23B that, when homozygous, suppresses all trichomes. The near-isogenic lines Tift 23B Tr Tr and Tift 23B tr tr have been used in studies to compare the pleiotropic effects of the *Tr* gene on several characters (Burton *et al.*, 1977).

A list of all the CMS lines that have been mentioned in the literature, irrespective of whether they have been used for commercial exploitation of hybrid vigor, appears in Table I. Reference will be made to some of these CMS lines in subsequent discussions.

B. COMMERCIAL UTILIZATION OF CMS LINES IN F_1 HYBRID PRODUCTION

The discovery of CMS fulfilled a historical need for a viable and economic method of producing high-yielding grain hybrids in pearl millet on a commercial scale.

Mahadevappa and Ponnaiya (1966) crossed four inbred lines having good combining ability with four CMS stocks developed by Madhava Menon (1958). The range of grain yield increases from 15 hybrids was from 4.4 to 157% over the check variety CO.1, and four were significantly superior to the check.

Seed of male-sterile Tift 23A and its maintainer Tift 23B was made available to breeders in India in 1962 (Athwal, 1966); seed of Tift 23DA and B and Tift 18A and B was made available in 1964 [Indian Council of Agricultural Research (ICAR), 1966; Utkhede, 1972].

The first five grain hybrids to be made on CMS Tift 23A, by the millet botanist at Ludhiana, were evaluated at six locations in 1963 and

TABLE I. Cytoplasmic male-sterile lines in pearl millet

Cytoplasmic male-sterile line	Remarks	Reference*
Tift 23A	Carries A1 cytoplasm	Burton (1965a)
Tift 23DA	Dwarf version of Tift 23A	Burton (1969)
Tift 23DA tr tr	Trichomeless, dwarf	Powell and Burton (1973)
Tift 23DEA	Early, photoperiod insensitive	Burton (1981a,b)
Tift 239DA	Carries A2 cytoplasm of L103A	Burton and Athwal (1969)
Tift 18A	Carries dormancy factor in seed	Burton (1965b)
L66A	Carries A2 cytoplasm	Athwal (1961, 1966)
L67A	Carries A3 cytoplasm	Athwal (1961, 1966)
L101A	Carries Tift 23A cytoplasm	Athwal *et al.* (1976)
L102A	Carries Tift 23A cytoplasm	Athwal *et al.* (1976)
L104A	Carries Tift 23A cytoplasm	Athwal *et al.* (1976)
L105A	Carries Tift 23A cytoplasm	Athwal *et al.* (1976)
L106A	Carries Tift 23A cytoplasm	Athwal *et al.* (1976)
L107A	Carries Tift 23A cytoplasm	Athwal *et al.* (1976)
L110A	Carries Tift 23A cytoplasm	Athwal *et al.* (1976)
L111A	Carries Tift 23A cytoplasm	Athwal *et al.* (1976)
L103A	Carries L66A cytoplasm	Athwal *et al.* (1976)
L108A	Carries L67A cytoplasm	Athwal *et al.* (1976)
L109A	Carries L67A cytoplasm	Athwal *et al.* (1976)
D202A	Selection in Tift 18A	Utkhede (1972)
18DA (126DA?)	Dwarf selection in Tift 18A	Vohra (1969)
28A	—	Utkhede (1972)
330A	—	Utkhede (1972)
558A	—	Utkhede (1972)
628A	—	Utkhede (1972)
5071A	Induced downy-mildew-reisistant mutant of Tift 23B	Pokhriyal *et al.* (1976)
5054A	A Nigerian line incorporating Tift 23A cytoplasm	Pokhriyal *et al.* (1976)
5141A	An Indian inbred incorporating Tift 23A cytoplasm	Pokhriyal *et al.* (1976)
5094A	A Nigerian line incorporating Tift 23A cytoplasm	Pokhriyal *et al.* (1976)
Pb 304A	Induced downy-mildew-resistant mutant of Tift 239DB	Gill *et al.* (1979)
Pb 405A	Induced downy-mildew-resistant mutant of L110B	Gill *et al.* (1979)
Pb 204A	Spontaneous downy-mildew-resistant mutant of Tift 23A and Tift 23B	Gill *et al.* (1981)
ICM ms81A	Induced downy-mildew-resistant mutant from Tift 23DB	Andrews and Anand Kumar (1982)
PT732A	An Indian inbred incorporating PT819 (Bellary, India) cytoplasm	Appadurai *et al.* (1982)

*Not necessarily report of development of a male-sterile line.

gave yields of 40 to 113% more than did the checks. In addition, 256 hybrids, also on Tift 23A, were evaluated in a preliminary trial at six locations in which several hybrids showed significant yield superiority over the check. However, restoration of pollen fertility was far from satisfactory (ICAR, 1964). In 1964, new hybrid combinations were evaluated at 7 or 20 locations (Table II) and yield as percentage of check ranged from 175 to 200. One of these hybrids, Tift 23A × Bil 3B, was released under the name HB-1 (HB, Hybrid Bajra; "Bajra," pearl millet) for commercial cultivation in 1965. Another hybrid, Tift 23A × J15, was recommended for cultivation in the state of Gujarat.

In advanced hybrid Bajra Class I trials (with adequate moisture) and Class II trials (under limited moisture) conducted by the All India Coordinated Millets Improvement Project (AICMIP) during 1965–1966, HB-1 yielded 77% more grain than the check (1191 kg/ha) over 17 locations and 73% more grain than the check (1179 kg/ha) over 14 locations in the respective trials (ICAR, 1966).

The spectacular yield advances that were achieved as predicted (Burton, 1948; Athwal and Rachie, 1963) stimulated several breeders to make and test other new hybrid combinations using CMS Tift 23A, Tift 18A, Tift 23DA, and L101A among those available. This increased activity led to the identification of four more hybrid combinations, named HB-2 (Tift 23A × J88), HB-3 (Tift 23A × J104), HB-4 (Tift 23A × K560), and HB-5 (Tift 23A × K559), between 1967 and 1972 (Table III). As the number of superior hybrids bred increased, the area planted to these also significantly increased. Of an estimated 12 million ha planted annually to pearl millet in India, the percentage of total area planted to hybrids increased from 3.3 in 1967–1968 to about 16 by 1971–1972 (Table IV). With the adoption of hybrids, production

TABLE II. Performance of some promising pearl millet hybrids, AICMIP, rainy season, 1964[a,b]

Pedigree	Grain yield (as % of checks)	Number of locations
Tift 18A × Bil 2A	200	7
Tift 23A × S 350	185	7
Tift 23A × Bil 3B	188	20
Tift 23A × CM63	175	20
L111A × Bil 3B	177	20
Check 1 (yield kg/ha)	735	7
Check 2 (yield kg/ha)	898	20

[a]AICMIP, All India Coordinated Millets Improvement Project.
[b]From the Indian Council of Agricultural Research (1966).

TABLE III. Pedigree of pearl millet hybrids released in India, 1965–1972, by AICMIP[a]

Hybrid	Pedigree	Year of release	Breeding site
HB-1	Tift 23A × Bil 3B	1965	Ludhiana
HB-2	Tift 23A × J88	1967	Jamnagar
HB-3	Tift 23A × J104	1968	Jamnagar
HB-4	Tift 23A × K560	1968	Kanpur
HB-5	Tift 23A × K559	1972	Kanpur/Delhi

[a]All India Coordinated Millets Improvement Project.

increased from 2.6 million metric tons in 1950–1951 to nearly 8 million metric tons during 1970–1971, with a corresponding increase in per hectare yields from 288 to 622 kg (Safeeulla, 1977). Among the hybrids released, HB-3 was by far the most popular hybrid because of its early maturity, bolder grains, and good performance under moisture-stress conditions.

India's pearl millet production then suffered a severe setback in the early 1970s due to epidemics of downy mildew caused by the fungus *Sclerospora graminicola* (Sacc.) Schroet, and by 1974 the production dropped to 3.6 million metric tons largely due to the effects of this disease (Jain and Pokhriyal, 1975; Murty, 1980). It became obvious that the epidemics were because of the common CMS line Tift 23A that was used in the production of all hybrids popular up to that time (Table

TABLE IV. Adoption of pearl millet hybrids in India, 1966–1967 to 1977–1978[a]

Cropping year	Total cropped area[b]	Hybrid adoption (%)
1966–1967	12,239	0.5
1967–1968	12,808	3.3
1968–1969	12,052	6.2
1969–1970	12,493	10.2
1970–1971	12,913	15.9
1971–1972	11,773	15.9
1972–1973	11,817	21.2
1973–1974	13,934	23.6
1974–1975	11,285	22.4
1975–1976	11,571	25.0
1976–1977	10,751	21.1
1977–1978	11,035	23.8

[a]From Swindale (1981).
[b]In millions of hectares.

III), which became so susceptible to downy mildew that it was no longer possible to grow it (Jain and Pokhriyal, 1975).

Efforts were directed initially at inducing resistance to downy mildew in Tift 23A and B through irradiation of Tift 23B seeds with 25 krad of γ rays, generating large numbers of plant(A) × plant(B) pairs and screening them for downy mildew resistance. At the sixth generation after irradiation, three A-line progenies were found that recorded no downy mildew incidence and were stable for CMS (Murty, 1973, 1974). One of these, named 5071A, showed a high degree of field resistance to downy mildew (Raut *et al.*, 1973; Pokhriyal and Jain, 1974), and with this line it became possible to reconstitute the original commercial hybrids. For example, HB-3 (Tift 23A × J104) was reconstituted and called NHB-3 (new HB-3; 5071A × J104). Likewise, the other hybrids, HB-4 and HB-5, were reconstituted and were named, respectively, NHB-4 (5071A × K560) and NHB-5 (5071A × K559). Seed of the reconstituted hybrids was multiplied for distribution to farmers; for example, Jain and Pokhriyal (1975) reported the multiplication of 600 metric tons of seed of hybrid NHB-5 (seed rate of 4 kg/ha) during 1974 to replace some of the then-existing downy-mildew-susceptible hybrids.

CMS line 111A (Table II) was found at the Punjab Agricultural University to show a high degree of resistance to downy mildew, and two resistant hybrids, PHB-10 (also called HB-6; 111A × PIB-115) and PHB-14 (also called HB-7; 111A × PIB-228), were released in 1975 (Gill *et al.*, 1975).

Thus the reconstituted versions of the "first-generation" hybrids (i.e., NHB-3, NHB-4, and NHB-5) and the two new hybrids (PHB-10 and PHB-14) developed on 111A were multiplied and successfully introduced into cultivation, thereby reducing downy mildew incidence considerably.

However, the success of the reconstituted hybrids was short-lived because CMS 5071A became rapidly susceptible to downy mildew, as did the reconstituted hybrids made with it. Sain Dass and Kanwar (1977) recorded, for instance, 29 and 39% downy mildew incidence on 5071A under natural and epiphytotic conditions, respectively, at the Haryana Agricultural University in Hissar, India. Further breeding efforts made at the IARI in New Delhi (Pokhriyal *et al.*, 1976) resulted in two new downy-mildew-resistant CMS lines—5141A and 5054A.

Two of the successful hybrids, HB-3 and HB-4 (which became NHB-3 and NHB-4 with 5071A as the female parent), were again reconstituted and renamed BJ104 (5141A × J104) and BK 560 (5141A × BK560-230), respectively, and were released for cultivation throughout India in 1976. Hybrid CJ104 (5054A × J104) and a dwarf hybrid, GHB-1399 (126D2A × J1399), were released for the state of Gujarat (Pokhriyal, 1977). Of these, BJ104, an early, high-tillering, and downy-mildew-resistant hybrid, has stability of yield and performs well under moisture-stress situations (Pokhriyal, 1977). In India, currently hybrids BJ104 and BK560 are widely grown, whereas CJ104 and PHB-14 are restricted to specific areas.

Of the limited number of commercially available CMS lines in India, 5141A is used in about 60% of the new hybrid combinations that are evaluated each year in AICMIP multilocational hybrid trials (Table V).

Research continues to develop other downy-mildew-resistant CMS lines in order to breed diversified hybrids to minimize future disease epidemics. Gill *et al.* (1977) were able to select for residual variation for downy mildew resistance in populations of Tift 23A (in a total population of 4000 plants) and Tift 23B (1000 plants) under natural conditions. One of the three CMS lines selected for downy mildew resistance resembles Tift 23A and has been designated as Pb 204A (Gill *et al.*, 1981). Andrews and Anand Kumar (1982) isolated an induced downy-mildew-resistant version of the highly susceptible dwarf CMS line Tift 23DA by irradiating seed of Tift 23DB. This was designated as ICM ms81A. (see Section II,A).

C. BREAKDOWN OF CMS

There are four reports (Vittal Rao, 1969; Reddi and Reddi, 1970; Thakare 1977; Saxena and Chaudhary, 1977) in which the stability of

TABLE V. Relative use of male-sterile lines in new hybrids tested by AICMIP, 1977-1979[a,b]

Male-sterile	No. of hybrids/year			Total	Percentage
	1977	1978	1979		
5141A	18	17	15	50	59
111A	5	3	2	10	12
5054A	2	3	2	7	8
5071A	1	—	2	3	4
Others	4	6	5	15	17
					100

[a]AICMIP, All India Coordinated Millets Improvement Project.
[b]From Coordinator's Report, AICMIP 1979-1980 (ICAR, 1980).

CMS lines has been compared in different seasons or years. In three studies it was found that environmental effects, principally temperature and humidity, can influence the frequency of plants shedding pollen. Thakur (1977), however, found no differences due to seasonal effects. It was also concluded that there may be genetic effects in which modifier genes can restore partial pollen fertility in an otherwise purely CMS line.

Pollen shedders in CMS 111A were eliminated by making plant(A) × plant(B) crosses and selecting in their progeny for stable male sterility (Gill *et al.*, 1977, 1979). The success achieved in breeding stable 111A indicates that modifier genes that restore fertility are present in certain male-sterile backgrounds and selection against them is possible.

Burton (1972) showed that fertile sectors discovered in heads of Tift 23A were a result of the occurrence of a dominant male-fertility-restoring mutation where one recessive ms_{c1} allele had mutated to Ms_{c1}. He also put forward the alternative hypothesis that fertile sectors could result because of the "mutation of A (sterile) to N (normal) cytoplasm."

Clement (1975), using four different CMS lines [ASM-3, derived from African material; LMS-1A (Tift 23A); and two sterile F_1 hybrids, ASM-5 (LMS-1A × male-fertile nonrestorer) and ASM-7 (LMS-1A × male-fertile nonrestorer)], observed several sectors of fertile anthers. ASM-3 showed the lowest rate of 0.03 fertile sectors/1000 heads, ASM-7 was highest with 1.17/1000, whereas ASM-5 and LMS-1A were intermediate, having rates of 0.26 and 0.15/1000, respectively. Hybrids obtained by crossing normal CMS plants × pollen from male-fertile sectors were all sterile, but selfed seed obtained from the fertile sectors produced fertile progeny, thereby indicating that the fertile sectors observed were due to cytoplasmic (plasmon) mutations.

Burton (1977) provided further evidence for the cytoplasmic nature of the fertile-sector mutants in sterility maintainers using CMS Tift 23A and Tift 239DA. He observed 103 male-fertile mutants that were the result of the cytoplasmic mutation that changed sterile (A) cytoplasm to normal (N) cytoplasm and hence made them male-fertile maintainers. These B (maintainer) lines resulting from such mutations appeared to be stable and identical to normal B lines in appearance and performance. The frequency of male-fertile mutations from CMS plants ranged from 1:431 to 1:737. In Tift 239DA, 219 plants with one or more heads were found that shed pollen in a population of 10,600 plants (slightly over 2%).

The evidence provided by Burton (1972, 1977) and Clement (1975) indicates that male-fertile plants or CMS plants with fertile sectors originate because of nuclear or cytoplasmic (plasmon) mutations. Obviously the gradual increase of male-fertile plants in a CMS line in a hybrid-seed-increase program would reduce the percentage of hybrid seed produced. Limited generation increase from breeders' seed and strict roguing offers the best methods of preventing both cytoplasmic- and nuclear-fertile mutants affecting the hybrid seed industry (Burton, 1977).

D. SOURCES OF CMS

Burton and Athwal (1967) reported the relationship between Tift 23A (Burton, 1965a) and L66A and L67A (Athwal, 1966) sterile cytoplasms. Genetic cytoplasmic interactions for fertility restoration or sterility maintenance as observed in the F_1 hybrids, originating from all possible reciprocal crosses between the sterile and maintainer lines, showed that the sterile cytoplasms carried by L66A and L67A are different from Tift 23A. L66B and L67B maintain sterility in Tift 23A, but Tift 23B restores fertility in both L66A and L67A. L66B restores fertility in L67A, and L67B is a partial fertility restorer for L66A. The ability of male lines to maintain sterility or restore fertility was visually estimated on the basis of percentage seed set by selfed heads and number of seeds per centimeter of head of the hybrid. The CMS Tift 23A, L66A, and L67A sources, since they carry different cytoplasms, were designated as S1, S2, and S3, respectively (Burton and Athwal, 1967), but the letter *S* was later substituted by the letter *A* because S1, S2, and S3 are normally used to describe the selfing generations (Burton and Powell, 1968). Burton and Athwal (1967) have also presented genetic models suggesting the relationship between different sources.

Aken'Ova and Chheda (1981) reported a CMS plant in a population of ex-Bornu "gero" (early) millet in northern Nigeria. To determine the relationship between the ex-Bornu CMS source and the three known sources in pearl millet, two plants (named Gero-1 and Gero-2) that were good maintainers for the CMS ex-Bornu were each crossed to Tift 23A1, 239A2, and 426A3. Gero-1 and Gero-2 were good maintainers for 426A3 and 239A2, respectively, but neither was a good maintainer for all three sources. The authors, however, suggest that the CMS source found in ex-Bornu may be different from the three previously known sources. Unfortunately, the maintainer lines are presently not available.

As noted earlier, crosses made with PT732A and B (Appadurai *et al.*, 1982) on other A and B lines indicate that PT732 may be a new CMS source.

Burton and Athwal (1967) found that L103B (maintainer of L103A developed from the same African source of cytoplasms as L66A) was a good fertility restorer for Tift 23A, in contrast to L66B, which maintained sterility in Tift 23A. Clement (1975), investigating the plasmon (cytoplasmic) mutations to male fertility on CMS lines, stated that the common assumption that the cytoplasm is the same for all stocks possessing the same maternal parentage is open to question and that there is likely to be considerable cytoplasmic variability in divergent lines originating from the same cytoplasmic source. The classification of male-sterile cytoplasms carried in different genetic backgrounds, if based only on the source of sterile cytoplasm (Athwal *et al.*, 1976), may therefore be erroneous when data on reciprocal relationships of restoration of fertility and maintenance of sterility are not included.

Burton and Athwal (1968), based on the reciprocal maintainer relationship that exists between A1 and A2 sterile cytoplasms, have proposed a scheme where population *Y* containing plants with A1 cytoplasm, and population *Z* containing plants with A2 cytoplasm and their maintainers, are used in a reciprocal recurrent selection program that facilitates the development of superior F_1 hybrids.

E. COMBINING-ABILITY TESTS WITH CMS LINES

Several studies were carried out to assess the general combining ability (GCA) of CMS lines in pearl millet (Table VI). The number of CMS lines involved in these studies ranged from 2 (Murty *et al.*, 1967; Appadurai *et al.*, 1980) to 7 (Kapoor *et al.*, 1979) and the testers from 9 (Ramadass *et al.*, 1974) to 184 (Murty *et al.*, 1967). Table VI indicates that though the same common CMS lines are involved in several studies, their combining-ability rating differs from researcher to researcher. For example, whereas Kapoor *et al.* (1979) and Yadav *et al.* (1981) have rated 5141A to be the best general combiner, Pokhriyal *et al.* (1976) rated 5054A better than 5141A. Likewise, Badwal *et al.* (1973) and Ramadass *et al.* (1974) found 111A to be best general combiner, but it was not rated as such by Kapoor *et al.* (1979) or Yadav *et al.* (1981). Pokhriyal *et al.* (1974) observed, contrary to predictions (Burton, 1969), that Tift 23A and Tift 23DA, which are near isogenic, showed wide differences in their combining ability.

Several of these researchers commented that the actual cross performance is decidedly more important when the development of the F_1 hybrids is the ultimate objective. This is because a CMS line, though rated as a good general combiner, may produce hybrids that are unacceptable for other reasons. This was illustrated clearly by Phul *et al.*

TABLE VI. Reports on combining ability of cytoplasmic male-sterile lines of pearl millet

CMS line involved*	No. of testers used	Better combiners (in descending order)	Reference
Tift 23A, Tift 18A (2)	184	Tift 23A (for tiller number), Tift 18A (ear length and girth)	Murty *et al.* (1967)
Tift 23A, L101A, L103A (3)	18	101A, Tift 23A, 103A	Gupta and Gupta (1971)
Tift 23A, L101A, L107A, L110A, and L111A (5)	10	111A, 110A, Tift 23A, 101A, 107A	Badwal *et al.* (1973)
Tift 23DA, Tift 18DA, Tift 18A, L110A, L111A (5)	10	110A, Tift 18DA, 111A, Tift 23DA, Tift 18A	Singh *et al.* (1974)
Tift 23A, Tift 18A, D202A, and L111A (4)	9	111A, Tift 18A, D202A, Tift 23A	Ramadass *et al.* (1974)
126D2A, 628A, Tift 23DA, 202A, and Tift 23A (5)	9	628A, Tift 23A	Pokhriyal *et al.* (1974)
L101A, L103A, L111A (3)	18	101 (forage characteristics)	Tyagi *et al.* (1974)
L101A, L103A, L111A, Tift 23A, Tift 23DA (5)	21	101A, Tift 23DA, Tift 23A	Tyagi *et al.* (1975)
5054A, 5094A, 5141A, Tift 23A, 5071A (5)	12	5054A, 5094A, 5141A, Tift 23A, 5071A	Pokhriyal *et al.* (1976)
67A, L111A, Tift 239DA, 628A (4)	19	628A, 111A, 67A, Tift 239DA	Phul *et al.* (1976)
Tift 23DA, L111A, 126DA, 5071A, 5054A, 5141A, and 5094A (7)	12	5141A, 5054A	Kapoor *et al.* (1979)
5141A and Tift 23DA (2)	40	No differences	Appadurai *et al.* (1980)
5141A, 5054A, L111A (3)	35	5141A, 5054A	Yadav *et al.* (1981)
5141A, 5054A, L111A (3)	16	5141A, 111A	Singh *et al.* (1982)

*Numbers in parentheses donote number of lines used.

(1976) and Pokhriyal *et al.* (1974), who found the CMS line 628A to be the best combiner, but the hybrids were tall, susceptible to downy mildew, and late in maturity. Murty *et al.* (1967) advocated individual performance of hybrids as the practical way of judging superiority, and Tyagi *et al.* (1974) also commented that a line with good general combining ability may not necessarily be better in all cross combinations. Ramandass *et al.* (1974) found that though 111A was the best general combiner for grain yield, the resultant hybrids were late in maturity, and those with Tift 18A, the second best combiner, were tall, with prolonged maturity.

The question that arises is whether the choice of testers used to evaluate the combining ability among CMS lines is appropriate. In some cases in which the objective is the replacement of a line (for example, the change of Tift 23A with 5141A to reconstitute hybrid BJ104) in a particular combination, obviously specific combining ability is of prime importance, and the most appropriate tester is the opposite inbred (J104 in the example cited) parent of a single cross (Matzinger, 1953). Development of new CMS lines is a time-consuming and laborious task, and ways are needed to determine at an early stage the worth of the newly developed CMS lines in hybrid combinations. During the process of CMS development it is a common practice to discard lines that have obvious morphological defects, unstable sterility, or susceptibility to diseases such as downy mildew. Phenotypic elimination of lines is effective for many traits that influence the commercial acceptance of hybrids, but to our knowledge effective elimination of poor combining lines by phenotype has not been achieved. Breeders test to identify unique hybrid combinations with high yields and stable performance, and it is here that the specific combining ability is expressed and capitalized.

F. INDUCTION OF CMS

Burton and Hanna (1976) reported the induction of CMS in pearl millet Tift 23DB using ethidium bromide. Male-sterile mutants (whole heads, sectored heads, or heads with sterile and fertile florets intermingled) occurred at frequencies of 1 in 30,100, 1 in 515, and 1 in 274 plants treated with 0, 250, and 100 ppm of ethidium bromide, respectively. The occurrence of sterile mutants in the generation that was treated, which set seed when pollinated and gave rise to CMS progenies, proved that the mutants were cytoplasmic in nature. They suggested that by this treatment the time and effort required to create and have CMS mutants in production would be much less than that required for the five or more generations of backcrossing now currently used. Furthermore, the utility of this approach would be in such cases as corn, in which the T cytoplasm carried by the CMS line conditions susceptibility to *Helminthosporium maydis* and the isogenic maintainer is resistant (Hooker, 1978). However, in pearl millet, Anand Kumar *et al.* (1983) have shown that the A1 type of male-sterile cytoplasm does not condition susceptibility to downy mildew and that it is the nuclear genes that are responsible for imparting resistance to CMS lines.

Burton and Hanna (1982) reported that treatment of Tift 23DB seed with aqueous solutions of streptomycin and mitomycin resulted in stable CMS mutants. Furthermore, the induced mutants were found to have sterility maintainer and fertility restorer requirements similar to Tift 23DA.

Hanna and Powell (1974) described a female-sterile mutant in Tift 23B subjected to thermal neutron treatment. This could be used to produce an obligate apomict, and they suggested a scheme for the production of hybrid seed, which presupposes a chromosomal rearrangement in which the female sterile segregates to give a 3:1 female-sterile to female-fertile ratio.

G. GENETIC MALE STERILITY

Genetic male sterility in pearl millet was reported by Gill *et al.* (1973) and Rao and Koduru (1978a) in which the male-sterile gene had no other effect except to cause abortion of the male germ cells. Rao and Koduru (1978b) showed that homozygosity for the gene *ms-2* produces, in addition to pollen abortion, plasmodial tapetum, plasmodial pollen mother cells, delayed and asynchronous meiotic development, desynapsis, and blockage of meiosis. Rao and Devi (1983) reported male sterility in lines Vg272 and IP482 that is controlled by a single recessive gene.

Genetic male sterility is the factor least used commercially of all the systems of sterility discovered in crop plants (Duvick, 1966), and this is also true for pearl millet. At the moment, genetic male sterility is of academic interest in pearl millet and may not be used because of the breeding system of the crop.

H. INDUCTION OF FUNCTIONAL MALE STERILITY

Hanna (1977) found that DPX 3778 (a methoxy triazine complex), prevented both anther exertion and dehiscence in pearl millet, but the pollen remained stainable and plump. A 7.43 kg/ha application at

the mid- to late-boot leaf stage, followed by a second application at the same rate 5-6 days later, reduced the selfed seed set to 2, 13, 5, and 30% respectively, in inbreds Tift 23DB, Tift 239DB, Tift 13, and Tift 18DB. Hanna (1977) suggested that DPX 3778 could be used for producing hybrids in pearl millet.

Sharma (1979) reported that a single foliar spray of 0.5% FW-450 solution was effective in inducing functional male sterility in a local strain (Bichpuri) of pearl millet. In the treated plants the emergence of anthers was delayed by a few days, and those anthers that emerged did not dehisce. Pollen and ovular fertility were not affected.

The availability of adapted CMS lines, though limited in range for maturity and height, has permitted new hybrids to be discovered in India. However, for areas in Africa where the Indian- or United States-bred CMS lines succumb to the high downy mildew pressure and CMS is not available in local backgrounds, the method of using male gametocides for producing hybrids may be feasible in the short term.

I. SCHEMES TO INCREASE THE FREQUENCY OF CMS MAINTAINER LINES

In recent years there have been proposals to develop "gene pools" of maintainer lines in pearl millet. These include the schemes to develop B-line synthetics (Andrews, 1976), maintainer or B-line complexes (Gill, 1979), and B composites (Rai and Andrews, 1980). All these proposals envisage the identification of superior maintainers and subsequent conversion through conventional backcrossing into CMS lines.

III. DEVELOPMENT OF CMS LINES AT ICRISAT

A. BREEDING DOWNY-MILDEW-RESISTANT CMS LINES

At ICRISAT, breeding of CMS lines was initiated in 1978 with a view to develop and distribute the lines to breeders in India and Africa as a support function in terms of providing them with means of identifying new hybrid combinations.

Conventional backcrossing is the technique (Allard, 1960; House 1980; Sharma, 1980) that has been used to incorporate sterile cytoplasm. The scheme that is routinely used for the development of new CMS lines involves (1) the grow-out of identified male-sterile testcrosses in two contrasting seasons, rainy and dry, to check the stability

of sterility, (2) breeding operations, at least from second or third backcross generations in the downy mildew nursery, and (3) generation of a large number of plant(A) × plant(B) crosses to allow selection for total male sterility, uniformity, and downy mildew resistance. It has been found that the frequency of maintainer lines is low: only 41 maintainers were identified after screening over 6000 testcrosses (about 0.6%) using the three standard CMS lines, 5141A, 5054A, and 111A (Table VII). These are at different backcross stages when a large number of plant(A) × plant(B) pairs are being handled for each CMS source under development.

In an effort to induce downy mildew resistance in susceptible Tift 23D2B, its seed was irradiated with 30 krad of γ rays in the rainy season of 1975. All the plants from the treated seed were selfed and planted as "head-to-rows" in the next generation. Each generation was grown in the downy mildew nursery where disease-free plants in the B line were crossed onto individual plants in the A line on a plant-to-plant basis. This process of pedigree selection and backcrossing was carried out to the sixth backcross generation in the rainy season of 1979, which corresponded to the eighth generation from the irradiation (Table VIII). At this stage three downy-mildew-resistant A and B pairs were identified based on uniformity, stable sterility, and other characters such as seed set and exertion, and their seed was increased in isolations. One of these CMS pairs was named ICM ms81A and its maintainer as ICM ms81B and was released to breeders in India through AICMIP in 1981.

The evaluation of a large number of plant(A) × plant(B) pairs in

TABLE VII. Frequency of maintainer lines in testcrosses on 5141A, 5054A, and 111A

Year	No. of testcrosses screened[a]	No. initially identified[b]	No. of maintainers confirmed[c]
1977	1655	168	5
1978	1513	78	0
1979	1266	102	27
1980	2000	9	9
Total	6434	357 (5.5%)	41 (0.63%)

[a]Rainy season.
[b]Based on rainy season observations.
[c]Based on rainy season and dry season observations.

TABLE VIII. Downy mildew incidence on sterile and fertile sixth-backcross progenies derived from mutagen-treated Tift 23D2B

Incidence class (%)	Relative frequency (%)		
	A lines (sterile cytoplasm)	B lines (normal cytoplasm)	Indicator[a]
0-10	61.5	62.8	0
11-20	27.6	28.6	0
21-30	7.3	5.3	4.5
31-40	2.4	1.3	4.5
41-50	0.5	1.0	0
51-60	0.3	1.0	9.1
61-70	0.3	0	13.6
71-80	0.1	0	27.3
81-90	0	0	18.2
91-100	0	0	22.7
Chi-square value	3.76[b]		
Probability range	0.75-0.50		
No. of progenies	1142	301	22

[a]Susceptible hybrid NHB-3.

[b]Numbers of progenies in the 41-60% incidence range were combined, as were those in the 61-80% range.

the downy mildew screening nursery provided data showing that the downy mildew incidence on A- and B-line progenies is not significantly different. This observation, coupled with the data provided elsewhere (Anand Kumar *et al.*, 1983), indicates that sterile cytoplasm has probably no role to play in determining downy mildew susceptibility. In

TABLE IX. Morphological characteristics of the three standard male-sterile lines and ICM ms81A[a]

Character	Male-sterile line			
	5054A	5141A	111A	ICM ms81A
Days to 50% bloom	50.7 ± 0.2	49.2 ± 0.1	57.8 ± 0.1	56.7 ± 0.2
Plant height (cm)	129 ± 0.7	131 ± 0.6	117 ± 0.7	82.7 ± 1.2
Ear length (cm)	17.4 ± 0.1	17.1 ± 0.1	28.1 ± 0.2	14.7 ± 0.2
Ear girth (cm)	5.5 ± 0.03	5.4 ± 0.03	6.3 ± 0.03	5.9 ± 0.05
No. of tillers/plant	2.7 ± 0.08	3.3 ± 0.08	1.4 ± 0.08	1.1 ± 0.02

[a]Recorded in rainy season 1980 at ICRISAT Center. Observations represent mean ± SEM and based on 100 plants for all except ICM ms81A (based on 72).

Table IX a summary of some of the morphological characteristics of the three standard CMS lines that are currently in use in India and ICM ms81A are presented.

Observations from many crosses with a wide range of diverse material indicate that the maintainer discovery rate is four times higher (around 2.5%) in crosses on ICM ms81A than that observed with the three standard CMS lines, which substantially increases the rate at which new CMS sources can be found. Experience in making hybrids using this dwarf male-sterile line indicated that it is a good combiner (in empirical terms), and the range of hybrid phenotypes that can be obtained is extensive.

B. INCORPORATING ERGOT RESISTANCE

All existing CMS lines are susceptible to ergot (*Claviceps fusiformis* Lov.) and smut (*Tolyposporium penicillariae* Bref.). In Table X ergot and smut reactions of two CMS lines and their respective maintainers are presented. ICRISAT millet pathologists have been able to identify and build up high levels of ergot resistance through selection in crosses between lines with low levels of resistance (since high levels of resistance could not be found in the world germplasm collection of pearl millet)

TABLE X. Ergot and smut reactions of two male steriles and their maintainers[a]

Head no.	Ergot severity (%)				Smut severity (%)			
	5141A	5141B	5054A	5054B	5141A	5141B[b]	5054A	5054B[b]
1	65	75	85	65	50	45	35	40
2	50	60	95	85	80	60	30	15
3	45	85	90	50	85	50	45	35
4	75	90	95	60	85	35	70	70
5	80	85	85	75	95	50	80	85
6	80	90	90	80	98	45	90	60
7	75	85	95	75	98	40	65	75
8	70	65	95	90	98	45	60	40
9	75	60	90	60	95	65	60	65
10	85	80	70	85	60	75	85	60
$\bar{X}$	70	77	89	72	84	51	62	54

[a]Recorded in the rainy season of 1981 at ICRISAT Center. Data courtesy of R. J. Williams and R. P. Thakur.

[b]In B lines (maintainer lines) individuals heads with low smut severity scores also had poor seed set.

(Thakur *et al.*, 1982). Evidence from this process and from crosses between resistant and susceptible lines indicates that the identified resistance is controlled by several recessive genes with cumulative effects.

The work on incorporation of ergot resistance into CMS lines has been carried out in two phases. In the first phase (dry season, 1980), 14 F_2 populations were derived using 10 ergot-resistant lines and 2 B lines, 5141B and 5054B. Over all the F_2 populations, the frequency of 0–10% ergot severity class (desirable) ranged from 0.5 to 62%. Though the frequency of ergot-resistant plants was relatively high (Table XI), from all the 14 F_2 populations only 73 plants (out of 5600 inoculated; 1.3% frequency) could be selected that combined good seed set and low ergot severity. These 73 were planted as F_3 progenies in the rainy season of 1981 and 10 heads were inoculated/progeny. In all, 52 individual plants could be selected that showed ergot resistance and good seed set. Progenies from these will be used for crossing onto the respective male sterile of the maintainer from which they were derived to assess their maintenance ability, for backcrossing to their respective B lines, and for intercrossing if necessary to increase the level of ergot resistance.

In the second phase, 66 new F_2 populations were generated, of which 22 involved two lines (ICMPE 134-6-9 and ICMPE 134-6-18) rated as "consistent" for ergot resistance. Fortunately, these two consistent ergot-resistant lines were found to be maintainers on ICM ms81A, thus opening up the possibility of converting these into CMS lines.

TABLE XI. Ergot severity in four F_2 populations from crosses between B line (maintainer) × ergot-resistant lines[a]

Ergot severity (%) class	Relative frequency (%) in F_2 populations[b]			
	Cross 3	Cross 7	Cross 8	Cross 9
0–10	62	8	45	45
11–20	8	1	10	10
21–30	8	7	8	10
31–40	7	12	12	11
41–50	6	10	7	11
51–60	3	5	6	4
61–70	3	11	8	5
71–80	3	24	4	3
81–90	0	14	0	1
91–100	0	8	0	0

[a]400 plants/F_2 population inoculated by millet pathologists.
[b]Based on observations on 200 plants.

C. INCORPORATING SMUT RESISTANCE

When the progenies derived from mutagen-treated 23D2B were grown at Hissar (a hot spot for smut) in the rainy season of 1977, it was observed that these, like all other CMS lines, were highly susceptible. To incorporate resistance, crosses were made between downy-mildew-resistant progenies of 23D2B and five smut-resistant lines in the 1978 dry season. Eighteen F_2 populations were grown at Hissar in the rainy season of 1980, and only those plants that were dwarf and had less than 10% smut severity were selected. Fifty-seven such F_3 progenies were grown in the 1980 dry season and testcrosses were made onto ICM ms81A to evaluate their maintenance ability. In the rainy season of 1981, the testcrosses and their corresponding F_4 progenies were planted at Hissar in the smut nursery. It was observed that the smut severity on F_4 progenies was much less compared to the testcrosses (Table XII). Of the 57 testcrosses, 16 scored for their fertile and sterile reactions at both Hissar and ICRISAT Center, were male sterile, and 14 of the remainder were partially sterile. The mean smut incidence was 47% on male-sterile testcrosses, which was significantly different from 33% observed on fertile testcrosses. From the data recorded it is evident that male fertility, i.e., pollination, has some effect on smut severity.

TABLE XII. Smut severity (%) on (23D2B-I × smut-resistant lines) F_4 progenies and their testcrosses, rainy season, 1981, Hissar[a,b]

Smut severity (%) class	Test cross		F_4 progenies	
	Number	Frequency (%)	Number	Frequency (%)
0–10	1	1.8	50	87.7
11–20	5	8.8	3	5.2
21–30	15	26.3	1	1.8
31–40	11	19.3	0	0
41–50	5	8.8	1	1.8
51–60	14	24.6	1	1.8
61–70	4	7.0	1	1.8
71–80	1	1.8	0	0
81–90	1	1.8	0	0
91–100	0	0	0	0
Total	57	—	57	—

[a]Ten heads were inoculated per entry by millet pathologists of ICRISAT Center.
[b]Testcrosses made on ICM ms81A.

D. HYBRIDS FOR AFRICA

As previously mentioned, CMS lines that are bred in either India or the United States are not suitable for most of Africa because they tend to be too early and are susceptible to downy mildew, ergot, and smut, in addition to insect pests.

At ICRISAT we have been able to identify maintainers in ex-Bornu (an improved landrace population from Nigeria), in Souna millets (from Mali), and in a Togo population (an early, large-grained variety); the latter two involve ICM ms81A cytoplasm. These and others such as a derivative of the cross J1623 × 3/4 ex-Bornu hold promise in the African situation for the development of adapted hybrids. Conducting further backcrossing during CMS line development in locations in Africa will aid in identifying disease resistances and other adaptation requirements.

IV. CONCLUSION AND SUMMARY

This article on cytoplasmic male sterility has largely concentrated on work carried out in India. The notable aspect of the history of the development and utilization of CMS in pearl millet is the simultaneous need that was felt in both the United States and India for a male-sterility mechanism for the production of commercial hybrids to exploit hybrid vigor. The discovery of male sterility was also almost simultaneous, and the first CMS line was made available in 1962. This made the production of pearl millet grain hybrids possible in India, which dramatically increased production. The downy mildew epidemic that ravaged the Indian pearl millet hybrid crop had its lessons, though not as much publicized as was the blight epidemic of maize in the United States. Breeders soon realized the need to replace Tift 23, which was highly susceptible to downy mildew, and they were eventually successful in finding replacements. Pearl millet production through the use of downy-mildew-resistant hybrids has again risen in India, and we consider this a remarkable achievement in such a short time.

Pearl millet hybrids in India are still based on the Tift 23A sterile cytoplasm, and efforts are being made both by breeders in Indian institutes and at ICRISAT to develop and use other CMS sources.

Work in progress at ICRISAT indicates the possibility of breeding and evaluating pearl millet hybrids using CMS lines that are adapted to Africa. If this leads to a positive outcome, the phenomenon of heterosis in specific combinations can be further exploited to increase grain production in another major region of the semiarid tropics.

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