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BREEDING FOR DISEASE RESISTANCE AND YIELD IN PEARL MILLET

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ABSTRACT

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We describe a program at ICRISAT, India, for breeding pearl millet for disease-resistance and high grain yield. Large-scale, reliable techniques for screening in the field for downy mildew, ergot and smut have been developed and are routinely being used. Since downy mildew is economically important, all breeding material passes through the downy mildew-screening nursery and resistant varieties and hybrids have been bred. Synthetic varieties have been produced which are also resistant to smut and are agronomically good.

Variability from African germplasm material, particularly for disease resistance, head volume, and seed size, has been exploited in crosses with Indian material. African parentage occurs in nearly all of the advanced breeding products of the ICRISAT program.

Recurrent selection has been used to produce open-pollinated varieties, one of which (WC-C75) is the first to be released in India where it already occupies a considerable hectarage. Conventional pedigree breeding has been used to produce synthetic parents, pollinators and seed parents. Several new seed parents have been released, and this broadens the genetic base of the hybrid crop which previously relied heavily on a single male-sterile line.

INTRODUCTION

Pearl millet, *Pennisetum americanum* (L.) Leeke (*P. typhoides* (Burm.) Stapf and Hubb.), is grown for grain and forage on about 26 million ha, principally in the tropical and subtropical areas of Africa and the Indian subcontinent (FAO, 1978). In low-rainfall, hot, sandy-soil regions it is the most important cereal, giving better and more reliable yields than sorghum or maize (Burton, 1983). Pearl millet is better adapted than other grain cereals to such adverse environments due to its ability to withstand high temperatures and severe moisture deficits, yet recover rapidly to exploit fully periods of favourable conditions (Bidinger et al., 1982). In comparison to other cereals this crop has hardly been exploited genetically for grain production despite its importance as a human food, its high nutritional value, resistance to adverse conditions and the availability of extensive, untapped genetic resources in both the cultivated and cross-fertile wild species.

In the late 1960s, when the first hybrids were grown in India, the first real evidence of the crop's food production potential was revealed, but also shown was the absolute necessity of breeding stable disease resistance into high-yielding cultivars. These first pearl millet hybrids, made possible by the discovery and utilization of cytoplasmic male-sterility (reviewed by Anand Kumar and Andrews, 1984), showed dramatic grain yield increases of 70% or more over existing varieties (ICAR, 1966). By 1971, over 2 million ha out of a total of 12 million were planted to hybrids when the first of several major epidemics of downy mildew (*Sclerospora graminicola* Sacc. Schroet.) occurred, which reduced production and restricted any further adoption by farmers (Safeeulla, 1977). From this experience and the known consequences of inbreeding on disease epidemics (Day, 1977), the research strategies adopted by the Pearl Millet Improvement Program at ICRISAT were directed towards finding diverse, and therefore possibly more stable, sources of disease resistance.

The first hybrids in India showed that plants which were early-maturing (75—85 days), of intermediate height (1.4—2.0 m), and high tillering (200 000—400 000 heads ha^{-1}) were capable of giving much higher grain yields, at all yield levels, than the plant types of the previously-existing Indian varieties. These new cultivars were remarkably widely adapted, from Tamil Nadu to the Punjab (9°N and 30°N, respectively). On the other hand, it was evident from the downy mildew epidemic of the early 70s (there have been others since) that there were difficulties in incorporating adequate downy mildew resistance into a single-cross hybrid where the two parents are both inbred lines. It was also apparent that such hybrids, as a class, are more susceptible to ergot (*Claviceps fusiformis*, Lov.) than open-pollinated varieties — a double-edged problem because ergot reduces yield and contaminates the grain, which renders it unfit for human consumption.

Higher levels of resistance to downy mildew (and other pests and diseases except ergot) were known to exist in Sub-Saharan West Africa, the area of largest genetic diversity and the likely centre of origin of pearl millet (Brunken, 1977; Brunken et al., 1977). There, landrace varieties, through coexistence with high levels of downy mildew, have developed genetic resistances which operate best in the natural varietal state of a random mating population. Plant to plant variability is clearly evident in every West African farmer's field. Although ergot can be found, and can be extremely severe on exotic lines in West Africa, local landraces avoid epidemics by pollen-based escape — the range of flowering usual within a varietal population provides an "umbrella" of pollen which reduces infection because, after fertilization and withering of the stigma, the floret is no longer susceptible. High levels of resistance to ergot could not be found directly but had to be developed through breeding (Thakur and Williams, 1980).

The ICRISAT program's responsibilities were to assist researchers in the semi-arid tropics with new data on breeding methods and techniques and in providing superior genetic material. Research was required on ways of developing hybrid parental material and varieties, by utilizing the derivatives of crosses between African germplasm and breeders' lines from India, Africa and the U.S.A. It was considered that varieties should be bred so as to incorporate or retain a range of resistance genes presumed to occur in landrace populations, while permitting the selection of high-yielding, heterozygous plants similar to the phenotype already known to be capable, in the early hybrids, of giving high yields over different environments. The breeding method chosen to accomplish this was recurrent selection on carefully constructed populations, using multilocational progeny testing, including exposure to high levels of downy mildew (and other diseases as necessary). The selection for disease resistance depended on the development of field-screening methods that were large-scale and reliable.

The disease susceptibilities of the early hybrids indicated that further progress in the breeding of hybrid parents must depend on the identification and incorporation of stable disease resistances into a number of genetically different parental lines. The genetic base of the hybrids could best be broadened in the seed parents, as very few of them were available. This would make possible the strategic deployment of different hybrids, to minimize the effect of the breakdown in disease resistance of any one of them. Traditional pedigree breeding methods were chosen to breed for hybrid parental lines and also in deriving the parental lines of synthetic varieties.

The work in the Pearl Millet Improvement Program commenced in 1973 at ICRISAT Center (17°N), and in 1975 at Hissar in the north (29°N) and Bhavanisagar in the south (11°N) of India. The experience gained by operating recurrent selection programs on the crop, which had not previously been attempted in pearl millet, and breeding parental lines was expected to result in the development of methodologies and material relevant to the improvement of the crop in Africa.

The resistance-screening techniques and the breeding methodologies used at ICRISAT in India can be adopted by other breeding programs. The purpose of this paper is, therefore, to provide a background to the methods used at ICRISAT, and to give an outline of the results so obtained. Some of this work has previously been reviewed (Williams and Andrews, 1983).

DISEASE RESISTANCE SCREENING TECHNIQUES

Downy mildew (*Sclerospora graminicola* Sacc. Schroet.), ergot (*Claviceps fusiformis* Lov.), smut (*Tolyposporium penicillariae* Bref.), and rust (*Puccinia penniseti* Zimm.) are important diseases of pearl millet in both Asia and

Africa (Rachie and Majmudar, 1980). In the breeding of disease-resistant plants, the first requirement is the development of screening techniques that reliably identify resistant genotypes. A field method is necessary where large numbers of plants are to be screened. It is desirable to use an inoculation method similar to that which occurs naturally, but which is capable of modifying environmental factors on which infection and disease development depend.

At ICRISAT Center, such large-scale screening techniques have been developed, and are being used to screen in the field for resistance to downy mildew, ergot, and smut.

Downy mildew

Traditionally, screening for downy mildew resistance has depended on 'sick-plots' which mainly utilize oospores in the soil for primary inoculum (Nene and Singh, 1976). Since sporangia also play an important role in the epidemiology of downy mildew (Bhat and Safeeulla, 1974; Singh and Williams, 1980), a field-screening technique was developed at ICRISAT Center, based on sporangia as the infection propagules (Williams et al., 1981). The technique depends on the production of sporangia on leaves of a susceptible cultivar, or mixture of two susceptible cultivars, planted as infector rows at regular intervals (every ninth row) throughout the field. Potted plants, which have been infected with downy mildew under controlled conditions, are placed at 10-m intervals in each 'infector row' to provide sporangial inoculum for the emerging infector plants. High humidity, a necessity for sporulation and infection, is provided by a mist irrigation system ("perfo-spray", Premier Irrigation Ltd., Calcutta) which is run for 15—20 min three to five evenings each week during the early growth stage (to first tillering) of the plants (Williams et al., 1981). Materials to be screened (test rows) are planted between infector rows when 30 to 40% of the plants in the infector rows are showing symptoms of systemic colonization by downy mildew, generally about 3 weeks after planting the infector rows. At regular intervals among the test rows 'indicator rows' of a susceptible cultivar are planted to monitor the intensity and uniformity of the disease pressure to which the test material is exposed.

The frequency of downy mildew-infected plants is recorded 15 to 25 days after sowing and again at the soft-dough stage. A severity index can be calculated based on the severity of the downy mildew symptoms of each plant (1—5 scale) after completion of heading (Williams et al., 1981).

Twelve hectares of downy mildew-screening nurseries have been maintained at ICRISAT Center each year since 1977, 6 ha during the rainy season and 6 ha during the post-rainy season. Hundreds of downy mildew-resistant lines have been identified in ICRISAT's genetic resources collection and in our breeding material.

Ergot

Ergot has recently assumed greater importance with large-scale, commercial cultivation of F1 hybrids in India (Thakur and Williams, 1980). Infection occurs through the stigma by air-borne ascospores produced from germinating sclerotia in the soil from the previous season's crop, and by conidia from the same season's crop (Thakur et al., 1984). Pollination before the application of inoculum has been reported to prevent infection (Thakur and Williams, 1980). Resistance-screening techniques proposed earlier (Reddy et al., 1969; Sundaram, 1969; Kannaiyan et al., 1972) did not eliminate such pollen-based escapes and therefore no confirmed resistance to ergot was reported.

At ICRISAT Center, an effective field-screening technique for identification of ergot resistance has been developed (Thakur et al., 1982). Macroconidia present in the 'honey dew' of infected inflorescences are suspended in water (10^6 conidia ml^{-1}) and sprayed onto protogynous inflorescences previously protected from external pollination by covering the heads at the boot-leaf stage with parchment-paper selfing-bags. The heads are immediately re-bagged after inoculation. High humidity is maintained by running overhead sprinkler irrigation twice daily during the period from inoculation to early grain filling. Inoculated inflorescences are scored for percent ergot severity 15—20 days after inoculation using a standard rating scale (Thakur and Williams, 1980). Selfed seed from inoculated inflorescences with little or no ergot are used for further evaluation and utilization.

An ergot-resistance-screening nursery is grown twice every year, 2 ha each in the rainy and post-rainy reasons at ICRISAT Center. The technique is highly reliable and may be transferrable to other locations. A large number of germplasm accessions and breeding lines have been screened, but adequate levels of resistance have not been detected. However, higher levels of resistance have been obtained by crossing the plants which are least susceptible to ergot and using pedigree breeding in the segregating generations which were screened in the ergot nursery (Thakur et al., 1982). These resistant lines are now being used in the breeding program.

Smut

Smut infection is reported to take place through the stigmas by sporidia which are produced from soil-borne teliospores (Bhatt, 1946). Several inoculation techniques have been tried involving a variety of inoculation times relative to flowering, types of inocula, types of bags to cover inoculated heads, and rating scales (Bhatt, 1946; Patel and Desai, 1959; Husain and Thakur, 1963; Pathak and Sharma, 1976). However, reliability was often lacking, resulting in little progress in the identification of resistant lines.

At ICRISAT, an effective technique for screening for smut resistance in the field has been developed (Thakur et al., 1983a). Sporidia produced on carrot/potato agar (Subba Rao and Thakur, 1983) are suspended in water (10^6 sporidia ml^{-1}) and inserted with a hand-held injector into the flag leaf sheath at the 'boot' stage. Heads, still in the boot stage, are immediately covered with parchment-paper selfing-bags and high humidity is maintained by running overhead sprinkler irrigation twice daily during the period from inoculation to early grain filling. Inoculated heads are scored for percent smut severity 20—25 days after inoculation using a standard rating scale (Thakur and Williams, 1980). Selfed seed from inoculated heads with little or no smut are used for further evaluation and utilization.

A 2 ha smut-resistance-screening nursery is maintained once a year in the rainy season at ICRISAT Center. The technique is highly reliable and can be transferred to other locations. Many lines from diverse geographic origins have been identified as smut resistant and these are being utilized in, for example, the breeding project for synthetic varieties.

Rust

Rust is not as serious economically as downy mildew, ergot or smut but it can cause serious reduction in forage quality. However, occasionally outbreaks can lead to yield loss of grain, and during the post-rainy season rust can be an important yield reducer in the production of hybrid seed.

Moderate to high levels of genetic resistance to rust are known, which are probably based on several genes. Resistance based on a single dominant gene, designated as Rpp1, has been found recently at ICRISAT (Andrews et al., 1985b). The stability of this resistance, however, has not been tested extensively. At present, screening for resistance to rust is done primarily at locations in India where the natural incidence of rust is invariably high.

Multiple disease resistance

Many lines have been identified as having resistance to two or more diseases. These were originally identified by exposing the same lines to disease pressure in more than one nursery. However, we are now able to screen for resistance to downy mildew, ergot, and smut by growing plants in the downy mildew nursery, where the reaction to downy mildew is determined, and inoculating separate heads of tillers of the same plants with ergot and smut to determine their reactions to these diseases. Several lines have been identified as having resistance to all three diseases.

Stability of resistance

The stability of resistance to disease is determined through multilocational testing in millet growing areas of India and Africa. Targeted entries are tested for downy mildew resistance in the International Pearl Millet Downy Mildew Nursery (IPMDMN), for ergot resistance in the International

Pearl Millet Ergot Nursery (IPMEN), for smut resistance in the International Pearl Millet Smut Nursery (IPMSN), and for rust resistance in the International Pearl Millet Rust Nursery (IPMRN). These nurseries have been in operation each year since 1976 or 1977, and sources of stable resistance have been identified for each of the four diseases.

GENETIC RESOURCES UTILIZATION

In a program to utilize new sources of genetic variability by hybridisation (the 'source material' project) the largest variation in the segregating generations has, in general, been found in crosses between Indian and African material. Indian landraces, or lines developed by Indian millet breeding programs, have mainly served as sources of earliness, higher tiller number, superior harvest index and local adaptation to Indian environments, whereas African material has been a good source of high head volume, large seed size, and disease resistances. Among African material, early groups have proved more promising in crosses at ICRISAT than late, photosensitive groups. The early groups are known locally, in West Africa, as 'Gero' or 'Souna' and the late groups as 'Sanio' or 'Maiwa'. An investigation into the pedigrees of about 1700 promising lines pedigree-selected up to the F_8 generation shows that the breeding populations per lines contributed much more to useful

TABLE 1

Some source material populations used in ICRISAT breeding projects

Population and source	Useful traits	Breeding products
Ex Bornu (IAR, Nigeria)	Long (30 cm), compact heads Downy mildew/smut resistance	Smut-resistant lines (as parents in crosses) Synthetic
3/4 Ex Bornu (IRAT, Niger)	d_2 dwarf Long (32 cm) compact heads Downy mildew resistance	R lines (as parents in crosses) B lines (as parents in crosses)
3/4 Hainei-Kirei (IRAT, Niger)	d_2 dwarf Very long (45 cm), compact heads Large head girth Downy mildew resistance	R lines (as parents in crosses) B lines (West Africa) Variety (West Africa)
Togo (Togo)	Early (48 days to flower) Large seeds (14 g per 1000) Large head girth White, cream, grey seed colour	R lines B lines Variety Synthetic parents

IAR = Institute for Agricultural Research.
IRAT = Institute de Recherches Agronomiques Tropicales et des Cultures Vivrières.

TABLE 2

Effect of recurrent selection on various characters[a] in six pearl millet composites

Composite	No. of cycles[b]	Grain yield			Downy mildew incidence (%)			Time to 50% bloom (days)			Plant height (cm)		
		Cycle		Gain per cycle[c] (%)	Cycle		Gain per cycle	Cycle		Gain per cycle	Cycle		Gain per cycle
		Co (tonnes ha^{-1})	Latest (tonnes ha^{-1})		Co	Latest		Co	Latest		Co	Latest	
Super Serere	5	1.93	2.11	1.8	2.1	1.0	−0.2	46.9	46.5	−0.1	222	221	−0.2
New Elite	3	2.36	2.57	2.6	1.4	0.0	−0.5	47.0	47.5	0.2	221	220	−0.1
Inter Varietal	4	2.11	2.39	1.9	1.9	1.6	−0.1	47.8	46.2	−0.4	221	213	−2.0
Medium	5	1.88	2.28	3.2	4.2	3.1	−0.2	45.2	43.4	−0.5	221	212	−1.7
Early	4	1.89	2.26	4.1	5.6	4.6	−0.3	38.8	40.3	0.6	189	193	1.0
D_2	2	1.97	2.27	5.0	7.5	4.9	−1.3	46.9	47.5	0.3	144	145	0.8

[a] Grain yield, time to 50% bloom, and plant height from mean of three locations.
Downy mildew incidence (%) from downy mildew nursery, ICRISAT Center, Patancheru.

[b] Data included only up to 1982.

[c] Gain per cycle (%) for grain yield calculated from regression analyses.

genetic diversification than the landrace accessions (Table 1). For example, 3/4 Ex Bornu and 3/4 Hainei-Kirei, both developed by the Institut de Recherches Agronomiques Tropicales et des Cultures Vivrières (IRAT) (Chantereau and Etasse, 1976), have contributed disease resistance, high head volume and the d_2 dwarfing gene.

Recently, the d_2 dwarfing gene has been introduced into seven, diverse, tall composites which have been used in the recurrent selection program at ICRISAT; preliminary yield trials have indicated that the d_2 dwarf versions of some of these composites have the potential to yield as much as, and even outyield, their respective tall counterparts. This now makes available a broad genetic base in a dwarf background for further exploitation in breeding dwarf, open-pollinated varieties and dwarf parents of hybrids.

Serere 10LA, a bold-seeded segregating line developed at Serere, Uganda, and, more recently, Togo landrace accessions are promising sources of earliness, large grain size (up to 14 g per 1000), early seedling vigour, and large head volume. Maintainer lines developed from Serere 10LA have made a remarkable contribution to the development of promising hybrid parents; direct selection from Serere 10LA has led to the development of male-sterile lines which are finding wide use in a number of millet-breeding programs in India.

A preliminary yield evaluation of open-pollinated varieties directly developed by intercrossing selected progenies from Togo accessions shows that these varieties have a high yield potential.

A general picture emerges of the great value of African material to the Indian breeding program. Moreover, African materials have been of most use when in the form of breeders' lines or populations, even though such materials have often only been selections from local landraces.

VARIETY BREEDING

Varieties derived from composites

At ICRISAT, recurrent selection has been carried out on many populations. Over the years, certain populations have been dropped and others merged. By the rainy season in 1983, six composites were being subjected to recurrent selection, and two to seven cycles of selection had been completed on them. The results of the comparison of performance of the Co (base) and advanced cycle bulks show that recurrent selection has been effective in bringing positive changes in gene frequencies for some important characters in all populations (Table 2). Genetic gains for grain yield from 1.8% (Super Serere Composite) to 5.0% (D_2 Composite) per cycle, equal to net gains of 200 to 400 kg ha^{-1} per cycle, have been obtained. Levels of resistance to downy mildew of all the composites, though good initially (and to smut in the Smut Resistant Composite), have also been im-

TABLE 3

Grain yield, fodder yield and downy mildew resistance of pearl millet variety *WC-C75 in* All India tests[a] from 1977 to 1983

	1977	1978	1979	1980	1981	1982	1983	Mean	Percent of BJ 104
Yield (tonnes ha^{-1})	(27)[b]	(33)	(23)	(27)	(30)	(24)	(30)		
WC-C75	1.63	2.07	1.76	1.85	1.99	1.85	1.79	1.88	101
BJ 104[c]	1.79	1.97	1.81	1.81	2.09	1.88	1.68	1.87	100
Local	1.36	1.92	1.61	1.47	1.42	1.86	—	1.61	86
Trial mean	1.54	1.95	1.68	1.73	1.92	1.78	1.69	1.76	94
Fodder (tonnes ha^{-1})	(23)[b]	(27)	(20)	(24)	(26)	(22)	(27)		
WC-C75	8.99	8.00	6.50	5.70	6.80	5.40	5.20	6.67	115
BJ 104	6.84	6.60	5.70	7.00	6.00	4.50	4.10	5.82	100
Downy mildew (%)[d]									
WC-C75	2.2	2.5	0.9	3.6	—	2.2	0.0	1.6	16
BJ 104	8.3	9.8	13.7	8.6	8.1	14.9	8.5	10.3	100
HB 3	93.5	72.3	42.1	—	—	—	—	69.3	—

[a]Data from the All India Coordinated Millets Improvement Project (AICMIP) Annual Reports.
[b]Number of test locations.
[c]The most widely grown hybrid in India (used as a check in variety trials).
[d]%downy mildew incidence from AICMIP pathology nurseries where HB 3 (or NHB 3) is the susceptible check.

proved over cycles. At the same time, maturity and plant height have been held more or less constant.

A new variety, WC-75 (also named by ICRISAT as ICMV 1), was developed from the "World Composite" by recurrent selection (Andrews et al., 1985a). It was tested in India by the Ministry of Agriculture, Government of India, and was released by them in May 1982. The performance of WC-C75 is shown in Table 3. The World Composite random mating population was constituted in Nigeria, in 1971, at the Institute for Agricultural Research, Ahmadu Bello University, from derivatives of numerous crosses between worldwide sources of pearl millet germplasm and Nigerian early-maturing landraces, locally known as 'Gero' millets. Full-sib recurrent selection was conducted on the World Composite at ICRISAT. During this selection, 441 full-sib families, derived from selected, heterozygous plants in the previous generation, were tested at Coimbatore (South India), Hissar (North India) and ICRISAT Center. Seven superior full-sib families were selected at Coimbatore, using supporting data from the other two locations. In the same season, disease-free plants from the seven full-sib families were selfed in the downy mildew screening nursery at ICRISAT Center. The resulting S_1 bulk was sown in the next season's downy mildew nursery, and bulk pollen was used to enforce intermating. The variety produced by this intermating was tested as WC-C75. In the five subsequent generations, before the production of breeder seed, a small proportion of the plants in the cultivar, which was naturally intermated in isolation, was discarded for poor agronomic characteristics.

Since 1975, when WC-C75 was bred, the varieties produced from the composites have improved. In the latest cycles of selection, yield advantages of 15—20% over WC-C75 have been recorded.

Synthetic varieties

The development of synthetics exploits heterotic combinations of parents while attempting to minimise inbreeding depression in the parental inbred lines. This is done by selecting a set of inbred parents which have good performance per se and which also have high general combining ability. Estimates of general combining ability have usually been made using diallel-cross techniques, although top-cross testing has also been used. This latter technique is less resource-consuming than a diallel cross. Research is in progress at ICRISAT to identify good, broad-based testers for use in top-crosses.

To derive potential synthetic parents, many crosses are made every year at ICRISAT and the subsequent generations subjected to pedigree selection. The parental lines of the synthetics are usually selected progenies from Indian × African crosses that are often between landraces and elite inbreds or varieties. As a result of continuous efforts, many progenies have been produced, some of them from the hybrid, recurrent selection, and genetic resources utilization breeding projects. All these progenies are screened in the downy mildew nursery at the F_4 stage and subjected to some test of combining ability. Groups of best combiners are selected, and random mating or diallel crossing of the selected set of lines, to generate a synthetic variety, is carried out in the downy mildew nursery. In 1980 to 1983, nearly 500 F_1's, 300 F_2's, 1000—2000 F_3 through to F_5 progenies, and up to 500 F_6, F_7 or inbred lines were evaluated yearly to identify superior parents for synthetics.

Synthetics developed in this project and tested in ICRISAT and the All India Coordinated Millets Improvement Project (AICMIP) trials, were found to be high-yielding and have better resistance to downy mildew than the standard hybrid, BJ 104. Two particularly promising synthetics, ICMS 7703 and ICMS 7704, were produced in 1977. ICMS 7703 was produced by random mating seven inbreds derived from Indian × African crosses: (1) (Souna D_2 × Ex Bornu)-2; (2) (J 25-1 × 700515-9)-2-3; (3) (B 282 × J 804)-1-3; (4) (J 25-1 × 700797)-5-3; (5) (J 260-1 × 700557-1)-4-9; (6) (J 1798 × 700594)-2; and (7) (700250 × Ex Bornu)-6. The "J" lines have their origin in India while the "700" lines and Ex Bornu originate from Nigeria, and Souna from Mali/Senegal. This synthetic has been tested in the AICMIP trials for 6 years and was recommended for release in 1984. It illustrates a common result in the breeding program, namely the success of Indian by African crosses.

Synthetics and disease resistance

In 1980, 12 F_5 lines showing low susceptibility to ergot were recombined to form three synthetics, of which one, ICMS 8034, was fairly good in yield (80% of BJ 104) and possessed high ergot resistance. In recent years, however, the agronomic worth of material with ergot resistance has been im-

TABLE 4

Performance of best seven entries in the pearl millet advanced synthetic trial, Kharif 1983

Entry	Grain yield (tonnes ha^{-1})						% over checks[b]	Downy mildew %[c]	Smut %[d]
	PHF[a]	PLF	BSR	HSR	Mean	Rank			
ICMS 8141	2.77	2.14	3.80	2.75	2.86	1	113 (107)	8.5	—
ICMS 8283	3.02	1.73	3.03	3.11	2.72	2	108 (102)	1.5	<1
ICMS 8120	3.00	1.73	2.95	3.07	2.69	3	107 (101)	4.5	—
ICMS 8019	2.69	1.91	3.03	3.06	2.67	4	106 (100)	2.0	—
ICMS 8137	2.90	1.98	3.11	2.60	2.65	7	105 (99)	4.5	—
ICMS 8148	2.57	1.89	3.14	2.81	2.60	8	103 (97)	3.5	—
ICMS 8282	2.94	1.30	3.26	2.78	2.57	9	102 (96)	2.5	<1
ICMS 7703[e]	2.54	1.61	3.47	3.06	2.67	6	106 —	0.5	46
WC-C75[e]	2.54	1.98	3.36	2.79	2.67	5	106 —	5.5	30
BJ 104[e]	2.86	1.72	2.31	1.96	2.21	24	88 —	12.5	52
S.E. ±	0.17	0.13	0.24	0.21					
Checks mean	2.65	1.77	3.05	2.60					

[a]PHF = Patancheru High Fertility; PLF = Patancheru Low Fertility; BSR = Bhavanisagar; HSR = Hisar.
[b]Figures in parenthesis on the basis of WC-C75 and ICMS 7703 only.
[c]Data from ICRISAT Centre, Patancheru downy mildew nursery.
[d]Data from ICRISAT Centre, Patancheru smut nursery, Kharif 1982.
[e]Check.

proved, and it is expected that ergot-resistant synthetics which are agronomically good will be bred in the near future.

The utilization of smut-resistant lines as parents of synthetics has paid quick dividends, as two synthetics, ICMS 8282 and ICMS 8283, derived from smut-resistant lines, have yields equivalent to the checks, WC-C75, ICMS 7703 and BJ 104, and have good smut and downy mildew resistance (Table 4).

HYBRID BREEDING

Breeding pollinators

The objectives of the hybrid project have been to generate variability by hybridisation between pollinators and subsequently to identify pollen parents that can produce superior hybrids with high and stable grain yields. Resistance to downy mildew is an important character, so all of the breeding material is screened at least once in the downy mildew nursery before the derived inbreds are test-crossed to seed parents. Potential pollen parents, produced from other breeding projects, are also tested, e.g. inbred lines produced from advanced composites, synthetics, or crosses with accessions from the genetic resources collection.

In the ICRISAT Pearl Millet Advanced Hybrid Trials (PMAHT) in 1978 and 1979 only four and one entry, respectively, were superior in grain yield to BJ 104. By contrast, 11 to 16 entries were superior to BJ 104 in the 1980 to 1982 trials. A reasonable, but untestable, explanation is that during the former period pollinators were mainly derived from pedigree breeding, whereas during the latter period pollinators also came from advanced composites in the recurrent selection program. An analysis of the pedigrees of pollinators that have reached the advanced trials shows that about 30% of them are derived from these composites, although these constitute a much lower percentage of entries in the initial trials.

Top yielding and agronomically acceptable hybrids from PMAHT are entered in the International Pearl Millet Adaptation Trial (IPMAT) for wider testing. Pollinators in the PMAHT which have moderate yield level, but are variable for plant height and days to 50% bloom, are reselected for uniformity and high yield by test-crossing 100 to 150 individual plants from the pollinator on to the male-sterile line of the parent hybrid. The progenies are first evaluated in an unreplicated test-cross nursery: the best lines are promoted to a replicated trial and then to an Elite Hybrid Trial (designated as PMEHT). The hybrids in PMEHT, therefore, have been derived from the hybrids entered in PMAHT and the reselection has been successful in improving their yields relative to BJ 104. These hybrids are also more uniform in height and days to 50% bloom. A disadvantage of such reselections is that during the additional generations required for reselection the seed parent used can become outclassed. Greater efforts are now made to obtain uniformity in pollinators, before crosses are made to the seed parent.

It is noteworthy that most of the elite pollinators developed by ICRISAT have some African material in their pedigrees and carry lateness in addition to good combining ability for yield and resistance to downy mildew.

Breeding male-sterile lines

Two promising hybrids, BJ 104 and BK 560 (both based on male-sterile line 5141A) were released by AICMIP in 1975 for widespread cultivation in India. The rapid spread of these high-yielding hybrids and the high general combining ability of 5141A (Kapoor et al., 1979; Yadav et al., 1981) led to the extensive use of this male-sterile line for the development of new hybrids. The vulnerability of hybrid breeding using a single male-sterile line was recognised and a male-sterile breeding project was begun at ICRISAT. Consequently a d_2 dwarf male-sterile line, 81A (also named by ICRISAT as ICMA 1) was bred and released in 1982 (Anand Kumar et al., 1984); it has a higher general combining ability than 5141A (Rai et al., 1985), and due to the extensive use of the downy mildew nursery during its breeding, it is highly resistant to this disease. Since 5141A has succumbed to downy mildew (Harinarayana, 1984), 81A is potentially an extremely valuable seed parent.

ICRISAT has made available to Indian millet programs two more d_2 dwarf male-sterile lines, 842A (also named by ICRISAT as ICMA 2) and 843A (ICMA 3) which have larger seeds and mature much earlier than 81A. Male-sterile line 842A was initially developed as AKM 2221, and 843A as AKM 2068 at Kansas State University, Fort Hays, KS. When tested in the downy mildew nursery at ICRISAT Center both were found to be highly susceptible with up to 46% of the plants infected. However, three seasons of reselection and A × B plant to plant crossing in the disease nursery led to the development of downy mildew-resistant versions of each, which have been jointly released by ICRISAT and Kansas State University (Stegmeier and Andrews, 1985). Initial test-cross evaluations indicate that these male-sterile lines have the potential of producing high-yielding hybrids in the early maturity group. Exploitation of a segregating line, Serere 10LA, has led to the development of a male-sterile line 834A (also known as S10A), which is a good general combiner in initial yield tests.

The male-sterile program at ICRISAT concentrates on dwarf male-sterile lines. Line 833A is another d_2 dwarf male-sterile derived from an Indian × African cross (J 1623 × 3/4 Ex Bornu) which has found wide acceptance with the Indian millet program, but is yet to be evaluated for its hybrid potential. The morphological features of these male-sterile lines are given in Table 5.

The work so far has been limited to nuclear diversification in the A_1 cytoplasmic system, which is likely to continue for some time as the sterility of the A_1 cytoplasmic system is the most stable among all the three cytoplasmic systems (A_1, A_2, A_3) reported by Burton and Athwal (1967). However, considering the genetic vulnerability of a narrowly-based, cytoplasmic sys-

TABLE 5

New male-sterile lines in AICMIP trial, ICRISAT Center, summer 1984

Characters	Male-sterile lines					
	5141A[a]	81A	833A	834A (S10A)[b]	842A (2221A)[b]	843A (2068A)[b]
Days to 50% bloom	51	61	44	49	49	42
Plant height (cm)	85	75	92	113	102	72
Head length (cm)	15	20	26	17	16	12
Head girth (cm)	5.2	5.2	6.6	8.6	6.8	6.3
Effective tillers per plant	4.0	2.3	3.2	2.6	2.1	4.1
1000 seed mass (g)	6.3	7.6	8.7	9.6	11.7	12.5

[a] Check.
[b] Synonyms.

tem such as that reported in maize (Hooker, 1978), attempts are now being made to diversify cytoplasmic systems in pearl millet. New sources of cytoplasmic male-sterile lines (S. Appa Rao, pers. commun.; L. Marchais, pers. commun.) are now being evaluated for cytoplasmic diversity and their usefulness in hybrid production.

Breeding ergot and smut-resistant hybrids

A large number of ergot-resistant lines were selected in the ergot-screening nursery and crossed on to elite male-sterile lines. All the hybrids so derived were susceptible to ergot. When ergot-resistant B lines were bred and used as the seed parents, then the hybrids with ergot-resistant pollinators were resistant: for example, 92% of F_1 hybrids from the female parent ER F_6—F_8 had less than 10% infection by ergot under test conditions. However, these hybrids did not yield as well as elite hybrids such as BJ 104 or ICH 220.

Ergot resistance appears to be recessive and controlled at a number of loci (Thakur et al., 1983b). It is difficult, therefore, to breed an ergot-resistant hybrid with high and stable grain yield. Backcross breeding is being done using elite pollinators and B lines as recurrent parents, and ergot-resistant pollinators and B lines as donors, respectively. The usual disadvantage of a backcross-breeding program applies, in that the recurrent parents may become outclassed while the backcross breeding procedure is being done, and it is unlikely that ergot-resistant hybrids can be bred equal in yield to the currently elite hybrids.

Hybrids produced between lines which are resistant to smut and a susceptible male-sterile line (81A) are susceptible, paralleling the situation in ergot. Although most of the smut-resistant lines had a smut severity less than 10%, the majority of the F_1 hybrids produced by these lines had a smut severity of 20—60%. There is again a need to produce both smut-resistant male-steriles and pollinators if smut-resistant hybrids are to be produced.

Reselection of BJ 104

After several hitherto resistant hybrids succumbed to downy mildew in India, hybrid BJ 104 (5141A × J 104) was released as a resistant hybrid for commercial cultivation in 1975. Its high yield potential and wide adaptability rapidly made it the most popular hybrid in India. Although it had some degree of susceptibility in downy mildew nurseries at the time of release, it showed high levels of resistance in farmers' fields until the early 1980s. Since then, there have been several reports of susceptibility of it and its parents (5141A and J 104) which has seriously reduced the yields of BJ 104 in several parts of the country.

To try to prolong the useful life of BJ 104, we selected for resistance within the parental lines. Both of the parental lines, although highly inbred, showed considerable phenotypic variability for susceptibility when subjected to high downy mildew pressure in a field nursery. Although the susceptibility of the two original lines was high, plants free from downy mildew and with phenotypes similar to the originals were found in each of them. The disease-free plants of 5141B were selfed and crossed to disease-free plants of 5141A. Ear-to-row progenies were grown in a downy mildew nursery and selections again made of symptomless plants. Two hundred and fourteen, 337, and 31 progenies of 5141B, 5141A and J 104, respectively, were subsequently grown, and a large number of progenies of 5141A and 5141B, but only five of J 104, remained free from downy mildew. Many progenies from the three lines were similar to the original lines, but only four A and B pairs and one J 104 progeny were selected as true-to-type.

These lines, and the hybrid made from them, showed high levels of downy mildew resistance under heavy, natural disease pressure in India in the 1983 rainy season. The lines are already being used by breeders in both the private and public sectors, and they are also being multiplied for the commercial production of a version of BJ 104 resistant to downy mildew.

CONCLUSION

Crosses between African and Indian germplasm, with intensive use of nurseries for disease screening of the progeny, have produced high-yielding downy mildew resistant varieties and seed parents for the Indian sub-continent. Identified sources of resistance to ergot, smut and rust have also been, or are being, incorporated into new varieties and hybrid parents in India and Africa. Recurrent selection based on multilocation progeny testing has been an effective method of combining yield and disease resistance with desired plant type in this crop. Experience gained on breeding methods, and the principles of operating field disease resistance screening nurseries are transferable and are being used in India and Africa.

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