Feature Articles

Pearl Millet

Pearl Millet Improvement at ICRISAT—An Update

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1. Introduction

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is one of the six crops for which the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) has responsibility to stabilize its grain yield at higher levels and serve as a world center for the repository of germplasm. Pearl millet is grown annually on about 26 million ha in the arid and semi-arid tropical areas of Africa and the Indian subcontinent, principally for grain but also for stover and forage. In these regions, which are characterized by low and erratic rainfall, high temperatures, low inherent soil fertility, and numerous biotic stresses, pearl millet is the most important cereal, giving higher and more stable grain yields than sorghum or maize. Pearl millet has a high nutritional value but its average grain yields are low (500-600 kg ha^{-1}), both in Africa and on the Indian subcontinent (Anand Kumar, 1989). Increasing the productivity of pearl millet in such low-yielding and unpredictable environments, to keep pace with the increasing food demand of the growing population in these regions, is a gigantic task requiring concerted efforts from the national and international research and development organizations.

ICRISAT initiated its pearl millet research in 1972 at its headquarters now the ICRISAT Asia Center, (IAC) located at Patancheru, near Hyderabad, Andhra Pradesh, India. Between 1976 to 1986, pearl millet improvement research supported by United Nations Development Program (UNDP) was conducted in collaboration with the National Agricultural Research Systems (NARSs) in the Sudan, Nigeria, Niger, Burkina Faso, and Senegal. In 1982, the ICRISAT Sahelian Center (ISC) in Niamey, Niger, was established to strengthen the research efforts in western Africa. In 1983, ICRISAT initiated its pearl millet research in southern Africa by establishing a Sorghum and Millet Improvement Program (SMIP) at what is now known as the Southern African Development Community (SADC)/ICRISAT Center at Matopos, near Bulawayo, Zimbabwe. To serve the needs of the eastern African region, ICRISAT established what is now known as the Eastern Africa Regional Cereals and Legumes Program (EARCAL) at Nairobi, Kenya.

The Cereals Program at ICRISAT took into account the following guiding principles to develop its pearl millet research strategy, some of which are common, of course, to the research programs of other ICRISAT mandate crops as well.

- From amongst the several grain yield-reducing factors, those requiring basic and strategic research attention should be clearly distinguished from those requiring immediate applied research attention.
- In prioritizing the research areas, those with high probability of success and the likely impact on increasing the grain yields and its stability on a larger scale should be accorded higher priority.
- Technology development should emphasize those components that are least affected by local environmental differences and hence are transferable across regions, are environmentally friendly, and have a high probability of adoption by the farmers.
- Research efforts should concentrate in those areas where the Institute has a comparative advantage stemming from its multidisciplinary team approach to problem-solving, access to diverse test locations, and its unique position enabling it to develop linkages with other international research organizations and mentor institutes that might be better equipped with the required scientific skills and/or research facilities.
- Research activities should be carried out in close collaboration and partnership with the National Agricultural Research Systems (NARSs) to strengthen their research capability, to avoid duplication of research efforts, and to jointly develop research priorities and strategies with focus on problems of regional significance.

In this update, we present the results of ICRISAT research on production constraints, genetic resources, genetic improvement, and cultivar development. We mention linkages with NARSs and with the mentor institutes in the UK and France, and briefly present the research results and activities of these collaborative arrangements. We shall refrain from presenting a compilation of everything that has been published and attempt to bring together the results of those publications that address major issues in a crop improvement perspective. In doing so we are aware of the exclusion from this update of some publications that might be important from other viewpoints.

2. Production Constraints

Poor harvest index (HI) of landraces was recognized as an important attribute requiring genetic improvement for increasing the grain yield potential of pearl millet. In addition, several biotic stress factors (diseases, insect pests and the root parasite *Striga*) and abiotic stress factors (drought and stand establishment) were also recognized as important production constraints requiring research for genetic improvement at ICRISAT.

2.1 Plant architecture. Pearl millet is a C_4 species with a very high photosynthetic efficiency and dry matter production capability. The traditional landraces are often tall, have thick stems, and are excessively leafy. While the biomass production of these landraces under the prevailing low-resource farming systems is very high (6-12 t ha^{-1}), their HI is often below 20% as compared to over 30% for the improved cultivars with high grain-yield potential (Anand Kumar, 1989). With a wide range of variability for various yield components available in the germplasm repository (see section 3.2), improvement in HI was logically recognized as the major thrust of breeding for higher grain yield.

Following the discovery of a cytoplasmic-genic male sterility (cms) system in pearl millet (Burton, 1958), grain hybrids with shorter plant height were developed in India, which had a HI of 40% and produced up to 8 t ha^{-1} of experimental grain yields in 85 days (Andrews et al., 1993). Also, the utilization of local landraces in breeding pearl millet topcross hybrids with higher HI, and consequently higher grain yields, has been demonstrated (Mahalakshmi et al., 1992a). Therefore, genetic improvement of HI while maintaining the existing levels of biological yields would substantially increase the grain yield potential of this crop.

Pearl millet may also be considered a crop likely to have a well-deserved niche in intensive agriculture. In Gujarat state of India, for instance, pearl millet is grown on a substantial area as an irrigated crop in the dry summer season, in which even short-duration hybrids give 25% higher grain yields than medium-duration hybrids when grown in the rainy season (Patel et al., 1987). Though under such farming systems, short-duration cultivars will be more appropriate, these will have lower biological yields than the medium-duration cultivars. It is possible to increase biological yields of short-duration cultivars by utilizing high growth rate characteristic of wild relatives of pearl millet (Bramel-Cox et al., 1986) for which a rapid field-screening method has also been developed (Bramel-Cox et al., 1984).

2.2 Downy mildew. Downy mildew (DM), caused by *Sclerospora graminicola* (Sacc.) Schroet., is the most destructive of all the diseases prevalent in the traditional pearl millet growing areas of Africa and the Indian subcontinent. This is evident from several epidemics on hybrids in India (see Dave, 1987; Rai, 1992b). DM also destroys much of the crop every year in Africa (Williams, 1984). Much of ICRISAT's research on DM pathology has concentrated on understanding the epidemiology and biology of the pathogen, development of effective large-scale screening techniques, and identification of sources with high levels of stable resistance.

Although the internal seed transmission of the disease has been a subject of controversy for a long time (Shetty et al., 1980; Williams, 1984), both the externally seed-borne and soil-borne inocula have been shown to be the sources of primary infection. The sporangia produced on infected plants play a major role in the secondary spread of the disease (Singh and Williams, 1980). The asexual phase of the pathogen, leading to the production of sporangia, is very efficient in that the sporangial cycle repeats every 24 h under favorable conditions, the number of sporangia produced per unit infected surface area is large, spore dispersal and dissemination is rapid, and spores can travel up to 340 m downwind during the rainy season with the disease spreading up to 80 m from the source of inoculum. Based on these findings, a large-scale field-screening technique (Williams et al., 1981) and a greenhouse seedling screening technique (Singh and Gopinath, 1985) were developed. These techniques have been further refined in subsequent years (S.D. Singh, personal communication).

Evaluation of >3000 germplasm accessions originating from more than 20 countries of the major pearl millet growing areas of the world led to the identification of several sources producing lines with high levels of resistance. These have proved stable in tests conducted across several locations in India and western Africa (Singh, 1990; Singh et al., 1987b). Some of the promising sources are listed in Table 1. Also listed in this Table are five additional inbred lines, initially developed from different (IP series) germplasm accessions as genetic stocks for various morphological marker traits, which have recently been found to be free of DM in tests conducted in disease nurseries in India, Niger, and Mali (Singh, 1992). Three of these resistant genotypes are different from the susceptible ones, especially in terms of reduced penetration of sporangia and zoospores (0-42% penetration in the resistant genotypes as compared to 100% penetration in the susceptible genotypes) after inoculation, restricted mycelial growth, and complete absence of haustoria formation (Chalam et al., 1992).

Recent research at IAC has discovered recovery resistance in which infected seedlings later outgrow the disease and develop into disease-free adult plants with all characteristics typical of the parental genotype. This type of resistance has been identified in a diverse range of materials including disease resistance sources, commercial cultivars and hybrid parents (Singh and King, 1988). A repeatable method of oospore germination has been developed, which will be useful in studies designed to evaluate the relative role of oospores and sporangia in disease development and host-plant resistance (Panchbhai et al., 1991). It has also been shown that substantial variability for host-specific virulence exists within a pathogen population whose quantitative virulence levels can rapidly increase even through asexual reproduction when repeatedly subjected to the same resistant host genotype (Thakur et al., 1992b).

Among the chemical control measures, seed treatment with metalaxyl (1-2 g a.i. kg^{-1} seed) has provided excellent control of DM (Williams and Singh, 1981) and its foliar application has a remissive property (Singh et al., 1984). Metalaxyl application at rates higher than 2 g a.i. kg^{-1} seed, particularly when applied in the form of seed dressing (Apron 35 SD) formulation, is toxic to seed germination. Pearl millet genotypes, however, differ in sensitivity to metalaxyl (Singh and Shetty, 1990).

The DM resistance of even the most successful single-cross hybrids in India has generally been overcome within 5-6 years of their initial large-scale cultivation. The resistant OPVs, in contrast, have generally been grown for twice as long without any significant reduction in their resistance levels, indicating the significance of OPVs in the stability of production and DM disease management. This difference between the susceptibility of single-cross hybrids and OPVs is related to the difference in (i) the levels of their genetic heterogeneity, (ii) the genetic base of these cultivars, and (iii) the previous selection history of the parental populations, in terms of the virulence levels of the pathogen populations to which they had been exposed. A preliminary study conducted in the disease nursery at IAC indicates that Tift $23A_1$ cytoplasm, currently involved in all the male-sterile lines used in commercial hybrids, is not associated with the susceptibility to the Patancheru isolate of DM pathogen population (Anand Kumar et al., 1983). The genetics of DM resistance is far from clear except that resistance generally displays partial to complete dominance over susceptibility.

2.3 Smut. Smut is a panicle disease, which is caused by *Tolyposporium penicillariae* Bref. It is relatively less damaging and widespread than DM. It occurs in all the African regions, in the northern part of the Indian subcontinent, and in the southeastern USA. High temperatures (20-35°C), high relative humidity (>80%), and long days (>12 h), seem to favor smut development (Thakur, 1990). The smut pathogen reproduces both sexually and asexually. There are no reports of biotypes or races in this pathogen, and the secondary spread of the disease within the crop is minimal because of a prolonged latent period of two weeks by which time flowering is almost complete (Thakur and Chahal, 1987). Due to protogynous flowering, pollination in pearl millet interferes with the infection by the smut pathogen, implying that cultivars displaying variability for flowering (e.g., open-pollinated cultivars) will contract less smut than the uniform cultivars such as single-cross hybrids (Thakur et al., 1983a). Hybrids based on cms lines are more susceptible to smut than those based on corresponding maintainer (B-) lines. This difference in susceptibility has largely been attributed to the male-fertility differences between the two groups of hybrids (Thakur et al., 1992a). Concerted efforts at IAC have led to the development of an effective field-screening technique (Thakur et al., 1983b) and diverse sources with high levels of stable resistance (Thakur et al., 1986). Some of the very promising sources are given in Table 1. Preliminary studies indicate that smut resistance is inherited as a partial to complete dominance with the number of genes not yet determined (Chavan et al., 1988).

2.4 Ergot. Ergot is also a panicle disease. It is caused by *Claviceps fusiformis* Loveless. Though more widespread than smut both in Africa and on the Indian subcontinent, it is normally a disease of secondary importance. The pathogen reproduces both sexually and asexually. The primary disease cycle begins with airborne ascospores discharged from the germinating sclerotia, which infect pearl millet at flowering (Thakur et al., 1984). Honeydew appears 6-7 days after infection. It contains numerous macroconidia that play an important role in the secondary spread of the disease. High RH (70-100%), an overcast sky with reduced sunshine hours, frequent drizzling rains, and cooler nights (18-20°C) are conducive for ergot development (Thakur, 1990). A greenhouse study showed that maximum ergot severity (61%) and minimum latent period (117 h) occur at a 30°C day/25°C night temperature regime with 24-96 h of panicle wetness (Thakur et al., 1991). An ergot severity threshold level of 20-30% in the field screening provided an adequate level of functional field resistance under artificially-induced ergot epidemic conditions (Thakur et al., 1989a).

Concerted efforts at IAC have led to the development of an effective field-screening technique (Thakur et al., 1982) and sources (lines and populations) with high levels of stable resistance to ergot (Thakur et al., 1985). Some of the very promising resistant sources are given in Table 1. Four ergot-resistant populations having additional resistance to DM and smut are also listed in this table. As in the case of smut, pollination interferes with infection by the ergot pathogen (Thakur et al., 1983c). Pearl millet pollen germinates much earlier than ergot conidia, leading to rapid pollination in the ergot-resistant lines that have short protogny. The pollination induces rapid stigma withering and consequently precludes ergot infection (Thakur and Williams, 1980). Willingale et al. (1986) suggest that pollination-induced stigmatic constriction provides an escape-based mechanism for ergot resistance. Several ergot-resistant male-sterile lines have recently been developed at IAC (K.N. Rai and R.P. Thakur, unpublished). High levels of ergot resistance observed in the inoculated and unpollinated panicles of these lines suggest that pollination-induced mechanisms are not the sole factor associated with ergot resistance.

Hybrids based on cytoplasmic-nuclear male-sterile lines are more susceptible than those based on their corresponding maintainer (B-) lines (Thakur et al., 1989b). The increased susceptibility of hybrids of A-lines, to some extent, is associated with higher levels of male sterility of these hybrids. Preliminary studies indicate that ergot resistance is inherited as a polygenic recessive trait (Thakur et al., 1983d), implying that breeding of an ergot-resistant hybrid would require both of its parents to be resistant to ergot, and probably also requiring that resistance in both parents be derived from a common source, which will reduce the probability of combining ergot-resistance and high heterosis for grain yields in hybrids.

2.5 Rust. Rust of pearl millet is primarily caused by *Puccinia substriata* Ell.& Barth. var *indica* Ramachar & Cumm. A number of species of *Puccinia* and races of *Puccinia substriata* have been reported as rust pathogens on pearl millet, but whether those occurring on the Indian subcontinent, in Africa and in the USA are the same or different is unknown (Singh and King, 1991). The occurrence of rust at the seedling stage can cause substantial losses in grain and fodder yields as well as fodder quality. From the viewpoint of grain production, rust is considered to be the least important of the four diseases occurring in the traditional pearl millet growing areas of Africa and the Indian subcontinent, owing to its appearance generally at the time of flowering or afterwards. Since the cooler climate favors the build up of high disease pressure, screening during the late rainy season planting under natural conditions has led to the identification of several sources with high levels of stable resistance (Table 1).

Genetic studies indicate resistance in one of these sources to be inherited as a monogenic dominant trait (Andrews et al., 1985b). In a study involving 12 rust isolates from India, western Africa, southern Africa, and the United States, among 12 pearl millet genotypes (7 resistant and 5 susceptible as reported in earlier studies), King (1991) observed differential reaction for pathogenicity among the isolates and for resistance among the host genotypes. Singh and King (1991) have reviewed the present global status of pearl millet rust research and suggested several research areas requiring future attention.

2.6 Insect pests. Pearl millet, in a global context, is reputed to have relatively fewer and less menacing insect pest problems than sorghum and maize. On the Indian subcontinent, especially in Rajasthan and Gujarat states of India, white grubs (*Holotrichia* spp) are the only serious pests that may require a significant research effort (Rachie and Majmudar, 1980). In many areas of western Africa, the situation is different. There pearl millet is

Table 1. Disease resistant pearl millet germplasm developed at ICRISAT Asia Center.

Disease	Resistant sources	Reference
Downy mildew	ICML 12, ICML 13, ICML 14, ICML 15, ICML 16	Singh et al. (1990a)
	IP 18292, IP 18293 IP 18294, IP 18295, IP 18298	Singh (1992)
Smut	ICML 5, ICML 6, ICML 7, ICML 8, ICML 9, ICML 10	Thakur and King (1988b)
Ergot	ICML 1, ICML 2, ICML 3, ICML 4	Thakur and King (1988a)
Rust	ICML 11	Singh et al. (1987a)
	ICML 17, ICML 18, ICML 19, ICML 20, ICML 21	Singh et al. (1990b)

attacked by a range of insect pests that damage the crop at all stages of its development (Sharma and Davies, 1988), leading to varying magnitudes of production losses. Even in this region, very few reliable estimates of crop losses due to insect pests are available (Nwanze, 1988), and the actual number that falls in the category of major pests of economic importance is perhaps less than a dozen (Nwanze and Harris, 1992). These include the earhead caterpillar (*Heliocheilus (= Raghuva) albipunctella* de Joannis), stem borer (*Coniesta (= Acigona) ignefusalis* Hampson), midge (*Geromyia penniseti* Felt), several species of grasshoppers, meloid beetle (*Psalyodolytta fusca* Oliv.), and scarabaeid beetle (*Rhinyptia infuscata* Burm). ICRISAT's research on pearl millet insect pests is conducted almost entirely in western Africa.

Stem borer larvae devour the leaf whorl by penetrating the main veins, then tunnel through the stem above the nodes, and finally feed on the stem pith. Subsequent desiccation of the central leaves results in deadheart formation. It completes 2-3 generations during a cropping season of 3-4 months. The adults emerge one month after the first rains. The main source of infestation is the diapausing larvae in the stems and stubbles of the previous crop season (Gahukar, 1984: NDoye and Gahukar, 1987).

Recent research on pearl millet stem borer pheromone conducted at ICRISAT Sahelian Center (ISC) in collaboration with the Natural Resources Institute, U K, has produced a cost-effective and environmentally friendly trap that could eventually be used in farmers' fields as a control strategy. The research focused on field experiments to optimize the attractive pheromone blend, to evaluate the efficacy and longevity of pheromones when dispensed from polythene vials, and to identify a suitable trap (ICRISAT, 1992). This research may have several immediate applications. It will be useful in large-scale monitoring of the insect population and their migration. It will also be cost-effective with easy access to the farmers, and will serve as an environmentally friendly component of an integrated pest management strategy.

The earhead caterpillar has become a major pest in the Sahel following droughts during the early 1970s. The female lays eggs near the developing grain and the larvae feed within the panicles. When the larvae are too big to squeeze between the involucre stalks, they bite through them leaving spiral tracks on the panicle. Fully grown larvae crawl down the stems and burrow into the ground where they pupate and remain in diapause until the following year. Farmers in the Sahel often lose 30-40 per cent of their produce due to the earhead caterpillars (NDoye and Gahukar, 1987). Recent research at ISC is focused on the biology, population dynamics, and development of effective screening methods.

Various pest control measures including cultural techniques, pesticides, resistant cultivars, and natural enemies have been evaluated to reduce crop losses due to pest damage. Nwanze and Harris (1992) have discussed various control measures and concluded that (1) chemical control would not be an appropriate strategy due to poor economic conditions of the farmers and the fragile nature of the ecosystem, (2) cultural control measures can be devised on the basis of existing information on biology and ecology of insects, although their widespread adoption and effectiveness would be hindered by the sociological and organizational constraints, (3) biological control measures, although requiring further investigation, may be difficult to apply in the critical climate of the Sahelian zone. This would leave host-plant resistance as the most cost-effective, environment-friendly, and widely acceptable control measure. A modest beginning has recently been made at ISC to develop this research area into a major integrated pest management component to contain the pest populations below economic threshold levels.

2.7 *Striga.* *Striga asiatica* (L.) Kuntze in India and southern Africa, and *Striga hermonthica* (Del.) Benth. in western Africa have been reported to parasitize pearl millet. *S. asiatica* is not considered a serious problem (Rachie and Majmudar, 1980). *S. hermonthica*, on the other hand, is the most widespread and damaging (Ramaiah and Vasudeva Rao, 1983). *Striga* seeds are tiny and are produced in vast numbers. They can remain viable in the soil for as long as 20 years, and go through a resting period before they can start germinating on the roots of the host plants. The seeds germinate in response to a stimulant produced by the host roots. *Striga* attaches itself to the host roots by haustoria. As the *Striga* plant develops, it takes over more and more of the host's root system. Even before it emerges, positive evidence of infestation is seen in the stunting of the host plant. If the infestation is severe, no panicles are produced.

Low soil fertility and low rainfall favor *Striga* infestation. A cultural control system for *Striga* that includes application of fertilizer nitrogen and farmyard manure, hand-pulling of the parasitic plant to prevent seed formation, and crop rotation with non-cereals is being studied at the ISC (ICRISAT, 1992). Selection for resistance to *Striga* in cultivated pearl millet has not yet produced any positive results. Considering that *Striga* has not been observed infesting *P. glaucum* subsp. *violaceum* (= *monodii*), which is a wild relative of pearl millet, 36 accessions of it were evaluated for *Striga* resistance at ISC during

1986 (Werder et al., 1989). Only two accessions had some degree of tolerance that needed further evaluation. The nature of *Striga* makes screening for host-plant resistance difficult. Pathologists usually use some type of 'sick plot' in a checkerboard pattern, with susceptible entries (controls) surrounded by test entries (Vasudeva Rao, 1985). When *Striga* resistant cultivars are identified, these could be included as a component in integrated control strategies (see also section 4).

2.8 Drought. Drought is the most important factor limiting pearl millet productivity. Studies on drought tolerance/resistance are complicated because of the uncertain nature of the frequency, duration and intensity of dry spells in relation to crop growth stages. There is paucity of reliable information on drought tolerance parameters, and also on the magnitude of genetic variability and heritability of these parameters.

Investigations conducted during the 1980s showed genotypic differences in their ability of abscisic acid accumulation (Henson et al., 1981) and osmotic adjustment (Henson et al., 1982) in response to water deficits. The utility of these traits in breeding for drought resistance/tolerance, however, was not evaluated. With flowering and early grain-filling demonstrated to be the crop growth stages most sensitive to water deficits (Mahalakshmi and Bidinger, 1985), physiology research at IAC has concentrated on this type of drought, which is variously known as end-of-season drought, terminal drought, and post-flowering drought. Beiler (1992) showed that terminal drought reduced grain yield by 50% with large variation among genotypes. This grain yield loss was caused by (i) reduction in grain size determined by a reduction in the grain-filling period and not the grain growth rate, and (ii) reduction in grain number affected by grain abortion. Studies at IAC (Bidinger et al., 1987) and ISC (Fussell et al., 1991) suggest that grain yield potential and earliness account for >50% of the genotypic variation for grain yield under terminal drought stress. The drought response index (DRI), a measure of drought tolerance, was less important than earliness in both the studies. Threshing percentage (ratio of grain to panicle yield) is a better indicator of terminal drought tolerance that, in conjunction with grain yield potential and earliness, accounts for >80% of the genotypic variation in grain yield under terminal drought stress (Bidinger and Mahalakshmi, 1993). Preliminary studies indicate that selection based on threshing percentage under terminal drought stress was effective when selected materials were evaluated in the same selection environment, but this selection was not effective when the selected materials were evaluated at other locations under terminal stress. Terminal drought has no effect on the assimilate partitioning of hybrid BK 560. Mahalakshmi et al. (1992b) showed that about 25% of the pre-anthesis assimilates and >95% of the post-anthesis assimilates were translocated to grains with their distribution pattern unaffected by water deficit during the grain-filling period.

In a line-source system of sprinkler irrigation applied to a wide range of genotypes, a linear decline in grain yield in response to the increasing severity of terminal drought stress is observed (Mahalakshmi et al., 1988). Also, estimates of grain yields and regression coefficients of a wide range of genotypes from line-source experiments correlate well with those from irrigated vs. non-irrigated experiments, indicating that the initial screening of genotypes can be effectively done by using the simpler irrigated vs. non-irrigated technique (Mahalakshmi et al., 1990).

2.9 Stand establishment. Poor plant stand is often a serious problem contributing to lower productivity of pearl millet. It may occur due to poor seed quality, poor seed bed preparation and sowing methods, poor seedling emergence, and reduced survival of emerged seedlings (Soman et al., 1987). High soil temperatures and soil surface crusting are, however, the two principal causes of poor seedling emergence and establishment. Both laboratory- and field-screening techniques for emergence at high temperatures have been developed and genetic variation for emergence has been demonstrated (Soman and Peacock, 1985; Soman et al., 1987; Lynch, 1993; Peacock et al., 1993). A field-screening technique for emergence through crusted soil surface has also been developed (Soman et al., 1984) and genetic variability, although of a much smaller magnitude than that observed for emergence at high temperatures, has been reported (Soman et al., 1987). A recent study showed significant heritability for seedling emergence both in pot- and field-tests in at least two of the four composites under evaluation, and there was a significant correlation between emergence in pots and in the fields (Witcombe and Soman, 1992).

Death of the emerged seedlings due to high soil surface temperature is another factor leading to poor stand establishment. A field-screening technique for seedling survival at high temperature has been developed and large variation among genotypes for seedling thermotolerance has been shown (Peacock et al., 1993). Genotypes with contrasting heat tolerance at the seedling stage have been observed to differ for heat shock proteins (Sivaramakrishnan et al., 1990).

3. Genetic Resources

ICRISAT serves as a world center for the repository of the germplasm of pearl millet and its wild and weedy relatives. The genetic resources activities at IAC include collection, evaluation, characterization, documentation, maintenance, conservation, and distribution for utilization of the germplasm held in its gene bank.

3.1 Status. By the end of 1993, ICRISAT had assembled 23 528 accessions of pearl millet germplasm from 46 countries, and 671 accessions of 23 *Pennisetum* species (S. Appa Rao, personal communication). A large proportion of this germplasm has been collected by ICRISAT in collaboration with NARS and the International Board of Plant Genetic Resources (IBPGR), now the International Plant Genetic Resources Institute (IPGRI). Germplasm collected by and maintained at other centers (e.g., National Bureau of Plant Genetic Resources and the Coordinated Millet Improvement Projects in India, and Institut francais de recherche scientifique pour le development en cooperation, ORSTOM, in France) were also assembled for conservation at ICRISAT. For the maintenance of this germplasm, a cluster bagging method is used (Appa Rao, 1980) and this activity is undertaken mostly during the dry season. The cluster bagging method produces a higher proportion of selfed seed than expected under sibbing. Considering the cost of hand-sibbing, when carried out with a large number of entries, and the risk of contamination associated with it, cluster bagging was proposed as the most practical method for the germplasm maintenance. Burton (1979), however, suggested an alternative method of germplasm maintenance in which the seeds of selfed panicles are bulked for each accession.

The formation of trait-specific gene pools currently underway is an additional technique for handling germplasm. Thus, 804 accessions, mostly from western Africa, are being random-mated to form a high head volume gene pool; and 887 accessions, mostly from Togo, Ghana, and Benin are being random-mated to form a large-seeded gene pool. Likewise, 1093 high-tillering accessions from diverse sources are being random-mated to form a high-tillering gene pool, and 1143 accessions from diverse sources are being random-mated to form an early gene pool (S. Appa Rao, personal communication).

Depending on the objective, three categories of seed storage facilities have been built at IAC (Mengesha et al., 1989). The short-term storage, meant for temporary holding, is maintained at 18-20°C and 30-40% RH. The medium-term storage, meant for holding active collections and conservation for 15-20 years, is maintained at 4°C and 20% RH. The long-term storage, expected to conserve seeds for >50 years, is maintained at -20°C. A medium-term storage facility has also been established at the ISC.

3.2 Diversity. Much of the assembled pearl millet germplasm has been evaluated at IAC during the rainy season following the methods given in 'Descriptors for Pearl Millet' (IBPGR and ICRISAT, 1993). The collection reveals a wealth of variability for numerous traits related to productivity, adaptation, quality, and several morphological characteristics. For instance, large differences among accessions have been observed for time to 50% flowering (33-140 days), plant height (35-475 cm), panicle length (5-165 cm), and 1000-grain mass (2.5-19.3 g) (Harinarayana et al., 1988). Considerable variability has been observed even within the populations. For instance, all possible panicle shapes were found in single pearl millet fields in Ghana (Appa Rao et al., 1985) and Malawi (Appa Rao et al., 1986b). Likewise, varying proportions of white and grey color seeds were observed in single fields in Cameroon (Appa Rao et al., 1988) and Zimbabwe (Appa Rao et al., 1989a). Inbreeding and selection in a highly DM-susceptible and early-maturing landrace (IP 2696) from Chad showed a wealth of variability, leading to the development of inbred lines with photoperiod insensitivity (S. D. Singh, unpublished), and high levels of resistance to DM (Singh et al. 1988) and rust (Singh et al., 1987a).

Sources of new dwarfing genes, earliness and photoperiod insensitivity, white and yellow grain color, glossy leaves, varying lengths of panicle bristles (up to 60 cm), high levels of resistance to DM, smut and rust, and low levels of resistance to ergot (Mengesha et al., 1990) have also been identified in the germplasm. Four sweet-stalk accessions have been identified, which have 13.5-19.4% soluble sugar (similar to controls) in the stalks at flowering and 8.5-11.9% soluble sugar (more than twice of controls) at maturity (Appa Rao et al., 1982). All these genetic resources could be of significant applied value in the genetic improvement of pearl millet. Sources of several interesting morphological marker traits such as bleached, midribless, glossy, zebra stripe, and narrow leaves; white leaf sheath; and numerous chlorophyll deficiencies have also been isolated from the germplasm (Mengesha et al., 1990), which will be useful in linkage and developmental studies. Anand Kumar and Andrews

(1993) present an excellent account of numerous qualitative characters and the genetics of many of these.

4. Genetic Improvement

With large genetic variability for various components of grain yield among the germplasm accessions, but with those components predominantly in undesirable genetic backgrounds, there has been need for recombination and selection for yield in desirable genetic backgrounds. A major activity in the genetic improvement of pearl millet at ICRISAT has been improvement of DM resistance. This was accorded an equally high priority due to (i) large genetic variation for pathogenicity in the pathogen population(s) and its enormous ability to rapidly produce and disseminate new recombinants, (ii) seriousness of the disease, especially on single-cross hybrids, (iii) availability of large-scale and effective screening techniques, (iv) numerous sources of resistance available in diverse and relatively good agronomic background, and (v) the dominant nature of resistance with high heritability. Although effective and large-scale screening techniques for smut and ergot were also developed, genetic improvement of resistance to these diseases received lower priority since their impact on grain yield reduction was much less than that of DM. Genetic improvement for ergot resistance received even less attention due to its complex inheritance, the narrow genetic base of available resistance sources, and its availability in relatively poor agronomic background. Rust received the lowest priority due to its minimal effect on grain yield. Genetic improvement of resistance to *Striga* and insect pests received no consideration at IAC as these are not serious problems on the Indian subcontinent. Until recently, lower emphasis on these in ICRISAT's western African regional program was due to preoccupation with genetic improvement for grain yield and DM resistance. Lack of (i) evidence of adequate and heritable genetic variability for resistance in the germplasm, and (ii) effective screening techniques, were also partly responsible for assigning low priority to the genetic improvement of resistance to these biotic stress factors.

Drought and poor plant stand establishment were recognized as the most serious abiotic stress factors both in Africa and on the Indian subcontinent. Genetic improvement for these factors, however, did not receive any significant attention because of the lack of evidence of adequate genetic variability for drought resistance/tolerance parameters, and the lack of demonstrated effectiveness of available screening techniques in selecting for resistance/tolerance.

The commercial cultivars of pearl millet, in general, have about 10% grain protein. Large variation for protein content has been observed in the breeding lines with some genotypes having up to 19.8% protein (Singh et al., 1987). A rapid screening method developed for seed protein evaluation of chickpea (*Cicer arietinum* L.) (Singh and Jambunathan, 1980) is available for large-scale routine application for pearl millet. A negative, but weak correlation, exists between grain yield and protein content, suggesting the possibility of simultaneous improvement in both traits (Kumar et al., 1983). In a grain yield improvement program, addition of the quantitatively-inherited protein content as another selection criterion would, however, lead to genetic slippage in grain yield improvement. Based on a nutritional survey in south Indian villages, Ryan et el. (1984) concluded that the prime need was for more of the energy supply and hence breeding for increased protein content or quality should not be undertaken if it were to hinder progress in the genetic improvement of grain yield. Ryan and Asokan (1977) also argued that large increases in cereal grain yields stemming from a grain yield-oriented plant breeding strategy itself would produce more nutrients per unit area. This, consequently, would lead to significant improvement in aggregate nutritional well-being of the consumers. As the grain protein content of the existing pearl millet cultivars is better than sorghum (Jambunathan et al., 1984) and grain yields are disappointingly low, breeding for higher protein content, initiated as a minor activity, was soon discontinued.

4.1 Selection in landraces. Due to relatively limited genetic variability for yield components within the landraces and the limited genetic gains historically achieved by selection within landraces in India, direct selection within landraces to develop open-pollinated cultivars and hybrid parents received little attention at IAC. The two exceptions are the development of a high-yielding and DM-resistant open-pollinated cultivar, ICTP 8203 (Rai et al., 1990; Rai, 1992b), and a large-seeded and DM-resistant maintainer line (ICMB 88004) from a northern Togo landrace (see sections 5.1 and 5.2). In both cases, the target environments for the resulting breeding products have been outside the area of origin for the landrace. Currently, we are exploring the utility of recurrent selection in populations developed using local landraces from the western part of Rajasthan, India to develop high-yielding cultivars, specifically adapted to the marginal production environment of this region where modern cultivars have not had any impact so far.

In western Africa, a relatively greater direct use of landraces has been made in the development of open-pollinated cultivars. For instance, IKMP 1 was developed by recombining selections made in several landraces from Burkina Faso. Similarly, IKMP 3 was developed from selection in landrace CVP 417, and IKMP 5 was developed from selection in landrace CVP 170, both from Burkina Faso. Another open-pollinated cultivar (ICMV-IS 88120) was developed from selection in landrace IP 6426 from Mali. Prolonged inbreeding and pedigree selection in landraces has been particularly useful in developing lines with highly enhanced levels of resistance to DM (Singh et al., 1988; Singh, 1990), smut (Thakur et al., 1986), and rust (Singh et al., 1987a), and photoperiod insensitivity (F.R. Bidinger, personal communication). Genetic improvement by this type of pre-breeding may, therefore, greatly increase the utility of landraces as parental materials in the breeding program.

4.2 Hybridization and pedigree breeding. Indian landraces and breeding lines generally provide excellent sources of tillering ability and earliness whereas African landraces and breeding lines provide excellent sources of several complimentary characters including large panicle size, high grain mass, sturdy stem, and resistance to DM, smut and rust. Thus, crossing between Indian (or Indian-type) and African materials became an important activity at IAC to generate a wide range of variability that could be utilized for the development of open-pollinated cultivars. Unlike the recurrent selection program, much of the selection at various stages of inbreeding in the pedigree program has been based on visual assessment for agronomic eliteness, grain yield potential, and DM resistance, mostly in unreplicated nurseries during the early generations and often during the advanced generations. The success of this breeding approach is evident in the release of a high-yielding and DM-resistant open-pollinated cultivar, ICMS 7703 (Jain et al., 1991), that was developed by crossing seven inbred lines derived largely from Indian-type × African crosses (see section 5.1).

African × Indian-type crosses have not proved productive in the breeding program at ISC as the latter group is susceptible to high temperatures at seedling emergence, is too early-maturing for a major part of the western African agroclimatic region, and is susceptible to all important diseases and insect pests. The attrition rate of African × Indian-type crosses was found to be very high. For instance, from over 500 plant × plant crosses involving 27 parents, only 17% of the original combinations involving only 12 original parents survived selection even as early as the F_3 generation. The use of individual plants in making crosses and selection among the F_1 s was a valuable breeding approach. Selection in a population derived from a cross between an Indian landrace from Ghana and a Souna landrace from Mali led to the development of an early-maturing and large-seeded OPV (GB 8735) at ISC.

Due to more stringent requirements for a number of agronomic and productivity traits in hybrid parents, especially seed parents (i.e., short height, good stalk strength, good seed set, high disease resistance,and high seed yield and good combining ability for grain yield), and the availability of such traits and trait combinations in existing elite inbreds, pedigree and pedigree-bulk breeding in populations derived mostly from Indian-type elite × Indian-type elite crosses and Indian type elite × African crosses continues to be the main breeding approach at IAC to develop hybrid parents. More than 1500 restorer lines of the A_1 cytoplasmic-nuclear male-sterility system, with a diverse range of morphological characteristics, have now been assembled in the pollinator collection maintained at IAC. One restorer line (ICMR 356), bred from an Indian-type elite × elite cross (B 282 × J 104) is the male parent of a high-yielding and early-maturing hybrid, (ICMH 356), which was recently released in India (see section 5.2). Twenty one male-sterile lines of varying morphological characteristics have been contributed by ICRISAT to the All India Coordinated Pearl Millet Improvement Projects (AICPMIP) since 1983. The maintainers of about half of these have been developed from hybridization and pedigree bulk breeding in populations derived from Indian-type elite × African crosses. Two widely-tested and particularly promising lines are ICMA 87001 and ICMA 89111, the latter being comparable to any of the highest-tillering male-sterile lines produced so far but having greater seed mass and DM resistance (Rai and Rao, 1992). A much wider range of non-restorers are currently at advanced stages of their evaluation and several of these are at various stages of their conversion into male-sterile lines.

During inbreeding and agronomic evaluation, intermittent exposure of breeding lines to DM in either the disease nursery or the greenhouse, or both, is an integral part of the total hybrid/parental lines breeding program. Such an approach has resulted in moderate to high levels of DM resistance currently available in improved agronomic backgrounds. Pedigree breeding in populations derived from crosses between B843 (the maintainer line of a commercial male-sterile line A843) and smut-resistant sources has been successfully used at IAC in the development of male-sterile lines with combined resistance to both smut and DM. The first d_2 dwarf, medium-maturing, and large-seeded male-sterile line (ICMA 88006) that has resistance to both DM and smut was contributed to AICMIP trial in 1989. Four additional male-sterile lines with resistance both to smut and DM were contributed to AICMIP trial in 1992, and several are at the final stages of their development. Pedigree breeding in populations derived from crosses between B843 and ergot-resistant sources has also produced about a half-dozen male-sterile lines with combined resistance to ergot, smut, and DM, one of which, (ICMA 91115 = ICMA 92666), was contributed to AICPMIP trial in 1992. The ergot-resistant male-sterile lines, unlike the smut-resistant male-sterile lines, have small seeds, a narrow genetic base, and are of medium height and medium maturity.

4.3 Recurrent selection. Recurrent selection is an ideal method of improving cross-pollinated crops. Pearl millet has several additional features, viz., bisexual and protogynous flowers, large number of seeds (up to 3000) per panicle, excellent tillering ability (4 to 6 tillers plant^{-1} under 75 × 50 cm spacing and good management), and low seed rate (3 kg ha^{-1}). These traits make pearl millet especially suitable for genetic improvement by recurrent selection. Taking these positive attributes into account and being aware of the greater vulnerability to disease epidemics of genetically uniform single-cross hybrids, IAC emphasized the formation and introduction of diverse composites for improvement by recurrent selection. The objectives of the program were (i) to produce high-yielding and DM-resistant open-pollinated cultivars and parental lines for hybrids, and (ii) to disseminate a diverse range of improved breeding materials to NARSs for utilization in their own breeding programs.

During the mid 1970s, as many as 20 composites of diverse origin, height and maturity characteristics, were subjected to recurrent selection at IAC. Based on grain yield potential, DM resistance, maturity, and the magnitude of genetic variability, some of these composites were dropped while the others were merged. Recently, several new trait-specific composites have been constituted for recurrent selection at IAC, ISC, and SADC/ICRISAT (Table 2). A recent multilocation-multiyear study of various cycle bulks of four composites (Rattunde and Witcombe, 1993) showed significant genetic gain for grain yield (3.6-4.9% cycle^{-1}) among three composites, which is comparable to those recorded for corn. These yield gains were achieved either by significant changes to shorter plant height and earlier flowering or without any change in plant height in two of the composites. Where DM incidence in the C_0 bulk was 8%, there was small but significant improvement in the DM resistance levels.

Since the composites had been improved by varying combinations of different selection methods (full-sib, half-sib, S_1 and S_2 progeny selection) with varying population size and selection intensity and with unequal number of test locations, comparison of various recurrent selection methods for their relative efficiency is not possible. A preliminary evaluation of 3-6 cycle bulks derived from the application of four selection methods (full-sib, S_2, gridded mass selection, and recurrent restricted phenotypic selection) in the World Composite did not reveal any significant difference in the effectiveness of these methods, implying that the breeding objective and resources available should play a more important role in the choice of breeding method (Singh et al., 1988).

4.4 Backcross breeding. The first major attempt of 'limited' backcross breeding at IAC was made in 1973 with the objective of converting, following a sidecar approach, seven diverse composites of medium to tall height into d_2 dwarf height. Comparison of seven pairs of tall and dwarf composites showed that dwarf composites had 35-43% shorter height than their corresponding tall composites (Rai, 1990). In five composites, there was no significant difference between the grain yields of tall and dwarf versions whereas in the two tallest composites (2.03-2.12 m height), the dwarf version gave 12-19% higher grain yields than its tall counterpart. The highest-yielding population in the trial was NCD2, the dwarf version of the Nigerian Composite. High levels of DM resistance identified in genetic stocks developed by ICRISAT's Genetic Resources Program (Singh, 1992) are being incorporated into a male-sterile line and two restorer lines of commercial hybrids. Genes for white grain color from diverse sources, and the d_2 and new dwarfing genes (Appa Rao et al., 1986a) are being backcrossed into common genetic background of elite inbred lines (E. Weltzien R., personal communication). Yellow grain color is being backcrossed into a grey-colored and bristled open-pollinated cultivar (Ugandi) that was released in Sudan. The e_1 gene for photoperiod-insensitive early-flowering has been transferred to an agronomically elite DM-resistant inbred line (ICMP 85410), which is an excellent restorer of both A_1- and A_m- cms systems (C.T. Hash, personal communication). Further transfer of this gene into a broad range of elite hybrid parents and late-maturing photoperiod-sensitive composites is underway. A recessive gene (*tr*) for the trichomeless trait is being backcrossed into three elite DM-resistant restorer lines and several elite DM-resistant maintainer lines. At ISC, the tr and brown midrib (*bmr*) genes are being backcrossed into three improved cultivars/local cultivars with an

Table 2. Major features of some pearl millet composites.

Composite[1]	Origin	Major features
I. ICRISAT Asia Center Composites		
African Population 88 (AfPop 88)	ICRISAT	Very late maturity, tall height, longpanicles, photoperiod sensitive
African Population 90 (AfPop 90)	ICRISAT	Late maturity, very long panicles, very vigorous
Bold Seeded Early Composite (BSEC)	ICRISAT	Early maturity, medium height, large seed size
Dwarf Composite (D2C)	ICRISAT	Dwarf height, medium maturity
Early B-Composite (EBC)	ICRISAT	Early maturity, medium height, large seed size, maintainer of A_1 cms
Early Composite (EC)	ICRISAT	Early maturity, medium height, good tillering
Early Composite II (EC II)	ICRISAT	Mid-early maturity, medium height
Early Composite 87 (EC 87)	ICRISAT	Early maturity, medium height, large seed size, moderate tillering
Early Composite 89 (EC 89)	ICRISAT	Early maturity, medium height, large seed size, moderate tillering
Early Composite 91 (EC 91)	ICRISAT	Early maturity, medium height, long panicles, moderate tillering
Early Rajasthan Population 91 (ERajPop 91)	ICRISAT	Very early maturity, high tillering, good adaptation to low yield environment
Early Smut Resistant Composite II (ESRC II)	ICRISAT	Early maturity, medium height, long panicles, smut resistant
Ergot Resistant Composite (ERC)	ICRISAT	Very late maturity, tall height, long panicles, ergot resistant
Ex-Bornu (EB)	Kano, Nigeria	Late maturity, tall height, long panicles
Extra-Early B-Composite (EEBC)	ICRISAT	Very early maturity, medium height, large seed size, maintainer of Am cms
High Growth Rate Population (HiGroP)	ICRISAT	Late maturity, medium height, high vegetative growth rate
High Head Volume B-Composite (HHVBC)	ICRISAT	Late maturity, dwarf height, large seed size, maintainer of Am cms (20-30% plants maintainer of A_1 cms)
High Tillering B-Composite (HTBC)	ICRISAT	Medium maturity, medium height, good tillering, maintainer of Am cms (20-30% plants maintainer of A_1 cms)
High Tillering Population 88 (HiTiP 88)	ICRISAT	High tillering, medium maturity, compact thin heads

Continued ....

Table 2. *Continued....*

Composite[1]	Origin	Major features
High Tillering Population 89 (HiTiP 89)	ICRISAT	High tillering, medium maturity, compact thin heads
ICRISAT Restorer Composite II (ICRC II)	ICRISAT	Medium maturity, medium height, medium panicles
Intervarietal Composite (IVC)	ICRISAT	Medium maturity, tall height, long panicles
Large Grain Population (LaGraP)	ICRISAT	Large grain size, medium height, mid-early maturity
Medium Composite (MC)	ICRISAT	Medium maturity, tall height, long panicles
Medium Composite 88 (MC 88)	ICRISAT	Medium maturity, medium height, large seed size, moderate tillering
Medium Composite 91 (MC 91)	ICRISAT	Medium maturity, medium height, large seed size
New Elite Composite (NELC)	ICRISAT	Medium maturity, tall height, long panicles
Nigerian Composite (NC)	Samaru, Nigeria	Late maturity, tall height, long panicles
Senegal Population (SenPop)	ICRISAT	Late maturity, tall height, long panicles, high vegetative growth rate
Smut Resistant B-Composite (SRBC)	ICRISAT	Medium maturity, medium height, smut resistant, maintainer of A_1 cms
Smut Resistant Composite (SRC)	ICRISAT	Late maturity, tall height, long panicles, smut resistant
Smut Resistant Composite II (SRC II)	ICRISAT	Medium maturity, tall height, long panicles, smut resistant
Super Serere Composite (SSC)	ICRISAT	Medium maturity, tall height, long panicles, large seed size
Western Rajasthan Population 88 (WRajPop 88)	ICRISAT	High basal and nodal tillering, small grain size, mid-early maturity
World Composite (WC)	Samaru, Nigeria	Medium maturity, tall height, long panicles
II. ICRISAT Sahelian Center Composites		
Early Maturing Composite (EMC)	ISC	Early maturity, medium height, medium-long panicles
Gray Seeds Intervarietal Composite (GRGB)	ISC	Medium maturity, medium-tall height, medium-long panicles, gray and white seeds
INRAN/ICRISAT Intervarietal Composite-2 (INMG-2)	INRAN/ICRISAT	Medium maturity, tall height, medium-long panicles

Continued ....

Table 2. *Continued....*

Composite[1]	Origin	Major features
INRAN/ICRISAT Intervarietal Composite-3 (INMG-3)	INRAN/ICRISAT	Medium maturity, medium-tall height, medium-long panicles
ISC Intervarietal Composite (ISC-851)	ISC	Medium maturity, tall height, long panicles
Long Head Gene Pool (LHGP)	ISC	Medium maturity, tall height, long panicles
Medium Maturing Composite (MMC)	ISC	Medium maturity, tall height, medium-long panicles
III. SADC/ICRISAT Composites		
Namibian Composite-90 (NC-90)	SADC/ICRISAT	Early maturity, medium height, good tillering
SADC Bold Grain Composite (SDBGC)	SADC/ICRISAT	Bold seeds, early maturity, medium height
SADC Bristled Composite (SDBC)	SADC/ICRISAT	Bristled panicles of variable size, medium to tall height, medium to late maturity
SADC Dwarf Composite (SDDC)	SADC/ICRISAT	Dwarf height, medium to late maturity, good tillering
SADC Early Composite (SDEC)	SADC/ICRISAT	Early maturity, medium to tall height, medium to long panicles, good tillering
SADC Late Maturing Composite (SDLMC)	SADC/ICRISAT	Late maturity, tall height, long panicles
SADC Medium Maturing Composite (SDMMC)	SADC/ICRISAT	Medium maturity, tall height, long panicles
SADC White Grain Composite (SDWGC)	SADC/ICRISAT	White-seeded, early to medium maturity, medium to tall height, long panicles, good tillering
Tanzania SADC Late Maturing Composite (TSLMC)	SADC/ICRISAT	Very late and photosensitive, tall height, long panicles

objective to derive near-isogenic populations. In collaboration with the International Livestock Centre for Africa (ILCA), the influence of these two traits on stover quality is being investigated.

During the applied backcross breeding program, isogenic lines can be developed for basic and strategic studies. Thus, 12 pairs of tall and dwarf near-isogenic lines were developed in the diverse genetic background of three composites. Evaluation of these inbred lines showed that the d_2 dwarfing gene, on an average, reduced the plant height by 42%, grain yield by 14%, and panicle girth by 8%; increased panicle length and number of panicles plant^{-1} by 5-6%; and had the least effect on time to 50% flowering and grain mass (Rai and Rao, 1991). This study also showed significantly large effects of the genetic background and environment on the relative performance of tall and dwarf near-isogenic lines, suggesting that the advantageous effects of the d_2 dwarfing gene can be effectively exploited by the manipulation of genetic background and selection in appropriate environments. In another study on six pairs of these near-isogenic lines, conducted at Tifton, Georgia in the United

States and at Patancheru in India, dwarf isolines had longer peduncles, longer and narrower panicles, thicker culms, wider leaves, and lower seed mass than their tall counterparts at both locations (Rai and Hanna, 1990a). The differences between the tall and dwarf isolines for total and effective numbers of tillers plant^{-1}, leaf sheath length, and time to 50% flowering were either not significant or were inconsistent across locations. Physiological investigations at IAC have shown that the d_2 dwarfing gene has no adverse effects either on coleoptile and mesocotyl length (Soman et al., 1989) or on sensitivity of grain yield and yield components to terminal drought stress (Mahalakshmi et al., 1991).

4.5 Mutation breeding. Tift 23A, the first cms line of pearl millet, developed at the Coastal Plain Experiment Station, Tifton, Georgia, USA (Burton, 1969) was introduced into India and used to develop the first commercial grain hybrid HB 1 (Athwal, 1965). This male-sterile line, however, became highly susceptible to DM and went out of commercial production in 1974 (see Dave, 1987). Selection for DM resistance in the disease nursery at IAC in the M_2 generation derived from gamma-irradiated seeds of Tift 23BD (developed at Tifton as a dwarf version of Tift 23B) led to the development of a DM-resistant maintainer line B81 (=ICMB 1) and its counterpart male-sterile line A81 (=ICMA 1) (Anand Kumar et al., 1984).

Comparative data on morphological traits (Rai and Hanna, 1990b) and molecular markers (Liu et al., 1992), however, do not preclude the possibility of introgression as the source of resistance in A81. In a cross-pollinated crop like pearl millet, the danger of cross-contamination is very high. For instance, the DM resistance of another male-sterile line (ICMA 841), assumed to have been derived from the residual variability in the commercial inbred seed parents A5141 and B5141 (Singh et al., 1992), resulted from introgression (Liu et al., 1992). From an applied viewpoint, both A81 and ICMA 841 continue to be resistant to DM and at present are the two most widely used seed parents of commercial hybrids in India (see section 5.2). Whereas ICMA 841 has its hybrid grain yield potential similar to that of A5141 (Singh et al., 1987b), the most widely used male-sterile line during 1977-1984, the hybrid grain yield potential of A81 is better than that of A5141 (Rai et al., 1986).

4.6 Cytoplasmic diversification. Much of the parental line breeding research in pearl millet has involved genetic diversification in Tift $23A_1$ cytoplasm (see Anand Kumar and Andrews, 1984; Rai and Singh, 1987). As a consequence, all the commercial hybrids at present are based on the Tift $23A_1$ cms source. A preliminary study indicates that this cms source is not associated with susceptibility to the Patancheru isolate of DM pathogen population (Anand Kumar et al., 1983). This study needs to be extended to diverse pathogen populations at other locations in India and Africa. In the meantime, new cms sources should be identified to diversify the cytoplasmic base of male-sterile lines to (i) sustain the hybrid program in case Tift $23A_1$ cytoplasm becomes susceptible to any disease or insect pest in the future, (ii) provide the option of converting those inbreds into seed parents that would be otherwise promising but are restorers of the Tift $23A_1$ cytoplasm, and (iii) exploit the advantageous effects of alternative cytoplasms, if any, on grain yield and other characters.

Besides several cms sources reported earlier (Rai and Singh, 1987), many new cms sources have recently been identified at IAC (Appa Rao et al., 1989b; Rai and Hash, 1993; K.N. Rai, unpublished). The mtDNA RFLP analysis of a few of those that have been studied shows one of these to be different from A_1, A_2, A_3, A_v, and A_m sources (Sujata et al., 1993). The utilization of this cms source (EGP 261) from the Early Gene Pool has led to the development of a highly DM-resistant male-sterile line ICMA 90111 (Rai and Hash, 1993). The utilization of the A_m cms source (Hanna, 1989) in breeding male-sterile lines has also begun. The utility of isonuclear lines in fertility restoration studies of hybrids for the reliable classification of cms sources has been shown (Rai and Hash, 1990), and the use of these isonuclear lines suggests that each of the 15 diverse ICRISAT composites/OPVs that were surveyed had varying frequencies of restorers of the A_m source (Rai, 1992a).

4.7 Biotechnology. Biotechnology at ICRISAT is viewed as a tool to supplement and assist the conventional crop improvement research. The emphasis at present is the adoption of available techniques rather than the development of new techniques. The biotechnological tools that have been considered relevant to the current needs at IAC are (i) application of tissue culture techniques for development of doubled haploids for genetic studies, (ii) restriction fragment length polymorphism (RFLP) analysis of mtDNA of new cms sources to facilitate diversification of the cytoplasmic base of hybrid seed parents, and (iii) construction of a RFLP-based genetic map of the nuclear genome to (a) characterize the pattern of molecular diversity among commercial cultivars and elite breeding lines, (b) identify molecular markers for genes responsible for resistance to diverse isolates of the

DM pathogen, thermotolerance, and other traits, and (c) compare recombination rates and segregation distortion resulting from male and female gametogenesis.

The application of mtDNA RFLP techniques (Sivaramakrishnan et al., 1991) to six cms sources identified from germplasm (Appa Rao et al., 1989b) grouped one of these with the Tift $23A_1$-system lines and five with L $67A_3$. A later study following the same technique suggested that A_v, A_m, and EGP 261 cms sources were different from each other as well as from the Tift $23A_1$ source (Sivaramakrishnan et al., 1993).

The development of a RFLP map of the nuclear genome and mapping of quantitative trait loci (QTL) associated with DM-resistance genes is being conducted in a collaborative project involving ICRISAT, Cambridge Laboratory, Norwich, UK, and University of Wales, Bangor, UK. Considerable progress has been made in this area. Results indicate that the degree of polymorphism in pearl millet is similar to that in maize and 96% of the 174 marker loci studied can be assigned to seven linkage groups on a map length of 345 cM (Liu, et al., 1993). Map position of QTLs responsible for resistance to DM pathogen populations from India and several western African locations are now being identified (Jones et al., 1993). In another collaborative project between IAC and the AFRC Institute of Grasslands and Environmental Research, Welsh Plant Breeding Station, Aberystwyth, UK, progenies from two crosses between thermotolerant and thermosusceptible lines have been developed for the QTL mapping of genes responsible for thermotolerance, and transfer of the Cambridge Laboratory map to the F_2 population from the first of these crosses is nearly completed (C.T. Hash, personal communication).

5. Cultivar Development

Recurrent selection in composites and pedigree selection in populations derived from inbred × inbred and inbred × cultivar crosses are the two principal approaches that have been equally emphasized at ICRISAT. While the major objective of this activity has been to generate improved breeding materials in diverse genetic backgrounds for eventual dissemination to NARSs for utilization in their own breeding programs, the utility of these materials for cultivar development needed to be demonstrated by developing high-yielding and DM-resistant open-pollinated cultivars (OPVs) and hybrid parents at ICRISAT. Due to (i) the lack of a pearl millet hybrid seed industry in Africa, and hence the higher probability for adoption of OPVs on that continent, (ii) a relatively lower vulnerability of OPVs to diseases than hybrids, (iii) a perceived niche for the cultivation of OPVs on the Indian subcontinent, and (iv) an assumption that OPVs could be used as the base materials from which NARSs could derive hybrid parents to complement their hybrid programs, greater emphasis was initially placed on the development of open-pollinated cultivars. During the mid-1980s, however, increasing DM incidence in India on the most widely used male-sterile line A5141 (the female parent of commercial hybrids BJ 104 and BK 560), and the continuing paucity of diversity in both male and female parents emanating from the Indian NARS' breeding programs led to the revision of OPV and hybrid breeding activities at IAC to make them more evenly balanced.

5.1 Open-pollinated cultivars. WC-C75, developed from the World Composite, is the first commercial open-pollinated cultivar (OPV) that was released in 1982 by the Govt. of India for general cultivation throughout the country (Andrews et al., 1985a). In the All India Coordinated Millet Improvement Projects (AICMIP) trials, this cultivar gave 99% of the grain yield and 120% of the dry stover of the then most widely grown commercial hybrid, BJ 104 (Table 3). WC-C75 was also highly resistant to DM (2% disease incidence as compared to 10% on BJ 104 in disease nurseries). During the period of 1984-1992, WC-C75 is estimated to have been grown annually on 0.6-1.2 million ha without any significant decline in DM resistance (C.T. Hash, personal communication). Three years later, another OPV (ICMS 7703), bred as a synthetic cultivar, was developed from inbreds, largely derived from Indian × African crosses. It too was released by the Govt. of India for cultivation throughout the country (Jain et al., 1991). With its grain yield and DM resistance comparable to WC-C75, release of ICMS 7703 was a significant development in the genetic diversification of improved cultivars at higher productivity levels.

Comparisons of OPVs developed from the later period of the synthetics program with those developed from composites undergoing recurrent selection showed the latter to be superior in grain yield and stability. Therefore, development of synthetic cultivars from inbreds was phased out at IAC. A large-seeded, high-yielding and DM-resistant OPV (ICTP 8203), developed at IAC from selection within a landrace from northern Togo, was released by the Govt. of India in 1988 for cultivation in Maharashtra and Andhra Pradesh states of India (Rai et al., 1990). This cultivar outyielded WC-C75 by 8% and flowered 2 days earlier in these two states during three years of AICPMIP trials (Table 3). ICTP 8203 became

Table 3. Mean performance of ICRISAT-bred open-pollinated cultivars in various All India Coordinated Pearl Millet Improvement Projects (AICPMIP) trials.

Trial/period	Number of tests	Entry	Grain yield (t ha^{-1})	Stover yield (t ha^{-1})	Time to 50% flower (d)	Plant height (m)	Downy mildew incidence (%)
Population trial (1977-80)	110	WC-C75	1.83	8.79	52	1.9	2.6
		BJ 104	1.85	7.33	48	1.7	15.8
Population trial (1979-83)	134	ICMS 7703	1.89	6.24	52	1.9	6.9
		WC-C75	1.85	5.92	51	1.9	2.3
Population trial (1986-88)	89	ICMV 155	2.10	6.80	55	1.9	4.8
		WC-C75	1.84	6.26	54	1.8	2.6
Population trial (1984-86)	30	ICTP 8203	1.81	3.56	52	1.6	1.3
		WC-C75	1.67	4.43	54	1.7	1.1
Population trial (1989-91)	79	ICMV 221	2.01	4.13	48	1.7	3.3
		WC-C75	1.76	4.80	52	1.8	3.9
Population trial (1991)	20	ICMV 221	2.25	3.70	44	1.6	2.5
		ICTP 8203	1.97	3.55	44	1.5	-

immensely popular with farmers in Maharashtra where it is estimated to have been grown annually on 0.6 to over 1.0 million ha during the period of 1989-1992. ICTP 8203 was also released in 1989 as PCB 138 in the Punjab state of India and as Okashana 1 in Namibia where it was estimated to have been grown on about 40 000 ha during 1989. ICTP 8203 and a sister OPV (ICTP 8202) along with other materials of similar characteristics were further utilized in developing a Bold-Seeded Early Composite (BSEC). ICMV 88908, bred from BSEC, is reported to have performed better than ICTP 8203, and hence is replacing the latter in Namibia (J.R. Witcombe and W. Lechner, personal communication).

Within 10 years of the release of WC-C75, another promising OPV (ICMV 155), developed at IAC from recurrent selection in the New Elite Composite, was released by the Govt. of India in 1991 for general cultivation throughout the country (Pheru Singh et al., 1993). This cultivar gave 14% more grain yield and 9% more dry stover than WC-C75 in the All India Coordinated Pearl Millet Improvement Projects (AICPMIP) trials (Table 3). With the plant height, time to 50% flowering and DM-resistance of both cultivars being similar, ICMV 155 is a likely replacement for WC-C75. Another high-yielding and large-seeded OPV (ICMV 221), developed from the BSEC at IAC, was released by the Govt. of India in January 1993. On an average, ICMV 221 gave 14% more grain yield and 10% more dry stover than ICTP 8203 in areas receiving 400 mm mean annual precipitation. With the plant height, time to 50% flowering, and DM resistance of both cultivars being similar, ICMV 221 is a likely replacement for ICTP 8203.

In the eastern African region, an UNDP-funded ICRISAT pearl millet research in the Sudan identified a bristled and early-maturing population (Serere Composite 2) having high grain yield. This composite, developed at the Serere Research Station, Uganda, was introduced into the Sudan via ICRISAT Center. In 11 trials conducted during 1977-1979 across 3-5 locations in central and western Sudan, Serere Composite 2 had an average grain yield of 1.06 t ha^{-1}, which was 56% more than Kordofani, the widely grown local cultivar used in the trials as the best local check (Jain and El Ahmadi, 1982). Based on its superior performance, Serere Composite 2 was released as Ugandi in 1981. In on-farm trials conducted during the 1984 in three villages in western Sudan, only Ugandi could produce plants with harvestable panicles. The average grain yield of Ugandi in these trials was 0.13 t ha^{-1} while the most common local cultivar, Baladi, produced no grain at all.

ICMV 82132, bred from an Smut-Resistant Composite at IAC, is the first smut-resistant OPV that was comparable to WC-C75 for grain yield in the AICPMIP trials. However, owing to its later maturity in the northern India, where smut affects pearl millet, however, this cultivar could not be released in India. In trials conducted later in Zambia, ICMV 82132 was found to have appropriate maturity and good grain yield potential. It was released there as Kaufela in 1989. Prior to this, another IAC-bred OPV (WC-C75) had also been released in Zimbabwe.

The Sorghum and Millet Improvement Program of SADC/ICRISAT developed a high-yielding OPV (SDMV 89004) by recombining S_1 progenies from C_o bulk the SADC Medium-Maturity Composite. This cultivar was released as PMV 2 by the Zimbabwean Department of Research and Specialist Services in 1992. PMV 2 has given 40% more grain yield than the local cultivars in yield trials at the experimental stations and twice as much as the local cultivars in farmers' fields. PMV 2 matures in 85-90 days compared to 110 days for the local cultivars.

In ICRISAT's African regional programs at ISC and SADC/ICRISAT, many more OPVs have been jointly developed in collaboration with NARSs (Table 4). Some of these are now beginning to reach farmers fields. In the western Africa, for instance, 12 OPVs in Senegal; 7 each in Burkina Faso and Niger; 6 in Cameroun; 4 each in Benin, Mali and Mauritania; 3 each in Ghana and Nigeria; and 1 each in the Republic of Chad and Togo, are either in on-station and on-farm tests, recommended for cultivation, or under cultivation by the farmers. Similarly, 6 OPVs in Zimbabwe, 4 in Namibia, 3 in Malawi, 2 in Tanzania, and i in Botswana, are either in on-farm trials or in demonstrations in farmers' fields.

5.2 Hybrids. ICMH 451, developed by crossing an IAC-bred restorer line (ICMP 451) onto an IAC-bred male-sterile line (81A) is the first commercially successful hybrid emanating from ICRISAT. It was released by the Govt. of India in 1986 for cultivation throughout the country. ICMH 451 gave 37% more grain yield and 21% more dry stover than BJ 104 in AICMIP trials (Table 5). ICMH 451 flowered 6 days later and was 0.2 m taller than BJ 104. It was also highly resistant to DM (1.3% disease incidence compared to 35.5% on BJ 104 in disease nurseries). Since 1988, ICMH 451 is estimated to have been grown annually on 0.6 to over 1.0 million ha in India. About a year after the release of ICMH 451, the Govt. of India released another promising hybrid (ICMH 423), which was developed at IAC by crossing an IAC-bred restorer line (ICMP 423) onto an IAC-bred male-sterile line (ICMA 841). In the AICMIP trials, this hybrid had grain yield and DM resistance comparable to MBH 110 (a popular commercial hybrid) but had 20% higher dry stover yield and was four days later to flower. ICMH 423, however, was not widely adopted due to the availability of hybrids of similar yield potential and morphological characteristics from the national breeding programs. One of these, Pusa 23 (also bred on ICMA 841), has been widely adopted.

In January 1993, an early-maturing hybrid (ICMH 356), bred at IAC by crossing an IAC-bred restorer line (ICMR 356) onto an IAC-bred male-sterile line (ICMA 88004), was released by the Govt. of India for cultivation throughout the country. The average grain yield of this hybrid was similar to that of ICMH 451, but ICMH 356 flowered a week earlier than ICMH 451 (Table 5). Significantly, ICMH 356 is based on parents whose DM resistance is derived from diverse germplasm sources. An informal collaboration between the pearl millet improvement programs of ICRISAT and the International Sorghum/Millets Collaborative Research Support Program (INTSORMIL) of the USA has made significant contributions, especially to the seed parents breeding activities of both organizations. For instance, an early-maturing and large-seeded male-sterile line AKM 2068, developed by the INTSORMIL's program at the Fort Hays Branch Experimental Station of Kansas State University, was introduced by ICRISAT and widely distributed in India as 843A (=ICMA 2). This male-sterile line was used by Haryana Agricultural University to develop and release a hybrid (HHB 67) that matures in 65 days. It is the earliest-maturing hybrid produced in India so far and is now a popular commercial cultivar. Further, the maintainer line of this male-sterile line (843B), owing to its early maturity, dwarf height, large seed size, and good general combining ability, has been extensively utilized in the hybridization program at IAC to develop a diverse range of male-sterile lines. Another male-sterile line (AKM 2221), again developed at the Fort Hays Branch Experiment Station and released in India as 842A (=ICMA 3), has greatly benefitted both public and private sector hybrid programs in India. Though several private seed companies in India appear to have developed their own hybrids on this male-sterile line, Chaudhary Charan Singh Haryana Agricultural University is the first public institution that has developed an early-maturing hybrid (HHB 68) on this male-sterile line. This hybrid was released in January 1993 for cultivation in Haryana, India.

Due to the lower susceptibility to diseases associated with heterogeneous OPVs and greater opportunities for the exploitation of grain yield heterosis and market potential associated with homogeneous single-cross hybrids, ICRISAT's pearl millet hybrid program has recently been conducting exploratory research on a compromise strategy of developing topcross- and three-way hybrids. A high-yielding and downy-mildew resistant topcross hybrid (ICMH 312), developed at IAC by crossing a restorer population (ICMR 312) on a male-sterile

Table 4. Status of improved pearl millet cultivars cooperatively developed by ICRISAT regional programs and NARS in western and southern Africa.

Country	Variety	Status
I. Indian Subcontinent		
India	RCB-IC 9	Released in 1991 for cultivation in Rajasthan
	RCB-IC 891, RCB-IC 892, RCB-IC 893, RCB-IC 901, RCB-IC 902, RCB-IC 911, RCB-IC 912, RCB-IC 924, RCB-IC 926, CZ-IC 912, CZ-IC 922, CZ-IC 923, CZ-IC 924, CZ-IC 315, GICV 91123, GICV 88921, GICV 92191, GICKP 92130, GICKV 92474, GICKV 91773, AIMP 92901, PCB-IC 148, PHB 138, GICH 91834	AICPMIP trials
II. Western Africa		
Benin	SOSAT-C88, ICMV-IS 88201 ICMV-IS 89305, ICMV-IS 86330	Advanced on-station trials
Burkina Faso	IKMP 1, IKMP 2, IKMP 3, IKMP 5, IKMC 1, IKMV 8201, ICMV-IS 88102	Recommended for cultivation by farmers in specific agroecological zones and planting conditions. ICRISAT has provided breeders and foundation seed to INERA. IKMV 8201 is popular and is adopted by farmers
Cameroun	IKMV 8201	On-farm tests and multiplication
	ICMV-IS 82212, ICMV-IS 89305, ICMV-IS 92222, SOSAT-C88, ICMV-IS 85321	Advanced on-station trials
Chad	ITMV 8001	Recommended for multiplication and general cultivation by the Service national de semences of the Ministry of Agriculture. Last reports (1989) indicate that this variety is grown on 45,000 ha and there is an increasing demand for seed
Ghana	ICMV-IS 88102	Seed provided to Global 2000 for on-farm evaluation
	ICMV-IS 88271, IKMV 8201,	Multiplied for on-farm trials and/or distribution to farmers
Mali	IKMP 1, IKMP 3, ICMV-IS 88102	Included on the official list of promising varieties and being multiplied for on-farm tests by extension agencies
	SOSAT-C88	Recommended for inclusion on official list promising varieties
Mauritania	ICMV-IS 85327, GB 8735, SOSAT-C88, ITMV 8001	On-farm tests by Centra national de recherche agronomique et de developpement agrocole

Continued ....

Table 4. *Continued ....*

Country	Variety	Status
Niger	ICMV-IS 88271, ICMV-IS 89201, ICMV-IS 89301, ICMV-IS 88201, ICMV-IS 85327, ITMV 8001	Service des Intrants du Controle de conditionnement et de la legislation Agricole (SICCLA) for evaluation
	ITMV 8001	On the list of recommended varieties, used in on-farm trials and on millet network demonstrations for farmers
Nigeria	ICMV-IS 89201, ICMV-IS 88210, ICMV-IS 88217	On-farm adaptative research trials by Brono State Agriculture Development Program
Senegal	IBMV 8001, IBMV 8004, IBMV 8401	Recommended for release in 1985. Seed is regularly multiplied of IBMV 8001 and IBMV 8004 and are grown in northern Senegal on an estimated 10,000 ha
	ICMV-IS 88217, ICMV-IS 88271, ICMV-IS 89305, ICMV-IS 88224, ICMV-IS 88305, ICMV-IS 86330, SOSAT-C88, ICMV-IS 89303	Seed provided to ISRA, Senegal, for on-station evaluation
Togo	GB 8735	Multiplied 2t seed and distributed to farmers by the Direction de la recherche agronomique
III. Southern Africa		
Botswana	SDMV 89004	Seed provided to the National Program for on-farm trials and demonstrations
Malawi	SDMV 89004, SDMV 89003, ICMV 88908	Under on-farm trials and demonstrations
Namibia	ICMV 88908	Released for cultivation throughout Namibia as Okashana I
	SDMV 89004, SDMV 90004, ICMV-F 86415, SDMV 90016	Recommended for on-farm trials and demonstrations
Tanzania	TSPM 91001, TSPM 91018	Seed provided to the National Program for on-farm trials and demonstrations
Zambia	WC-C75, Kaufela, Lubasi	Released for cultivation in Zambia
Zimbabwe	SDMV 89004	Released for cultivation throughout Zimbabwe
	SDMV 87001, SDMV 89001, SDMV 89002	Recommended for on-farm trials
	SDMV 89005, SDMV 89007, SDMV 89008	Recommended for demonstration for farmers

Table 5. Mean performance of ICRISAT-bred hybrids in the All India Coordinated Pearl Millet Improvement Projects (AICPMIP) trials.

Trial/period	Number of tests	Entry	Grain yield (t ha^{-1})	Stover yield (t ha^{-1})	Time to 50% flower (d)	Plant height (m)	Downy mildew incidence (%)
Hybrid trial (1984-85)	51	ICMH 451	2.20	5.8	55	1.7	2.3
		BJ 104	1.61	4.8	49	1.5	38.9
Hybrid trial (1983-86)	49	ICMH 423	2.07	5.9	53	1.7	4.4
		MBH 110	2.04	4.9	49	1.8	1.5
Hybrid trial (1985-86)	68	ICMH 423	2.10	5.5	54	1.6	4.4
		ICMH 451	2.27	5.8	56	1.7	1.5
Hybrid trial (1986-90)	59	ICMH 356	2.40	4.5	48	1.6	2.1
		ICMH 451	2.34	5.5	55	1.8	3.5

inbred line (81A), has given 5% more grain yield and flowered two days earlier than the commercial hybrid check (ICMH 451) in 95 replicated trials conducted over three years in India (B.S. Talukdar, personal communication). A recent study (Mahalakshmi et al., 1992a) shows that topcross hybrids developed by crossing locally adapted OPVs (landraces or improved cultivars) from western Rajasthan onto male-sterile lines had grain yields equal to or more than these OPVs in the low-yielding environments and were more responsive to improved environmental and management conditions. These findings indicate that some of the high-yielding OPVs may be utilized for improving grain yields through topcross hybrids.

IAC-bred male-sterile lines have also shown promise in breeding topcross hybrids for the southern African region. For instance, a preliminary trial consisting of 161 topcross hybrids, developed by crossing 23 SADC/ICRISAT-bred OPVs on 7 IAC-bred male-sterile lines, identified more than 30 hybrids outyielding PMV 2. The best topcross hybrid (SDMH 92012) had 1.66 t ha^{-1} grain yield, 54% more than the best OPV (SDMV 90025). The five top ranking hybrids were all based on the smut-resistant male-sterile line ICMA 88006. Almost all the male-sterile lines bred at IAC are highly susceptible to DM in western Africa. Development of male-sterile lines that are DM resistant in western Africa is currently underway at ISC. In the meantime, taking advantage of protogynous flowering, the use of male-fertile inbreds as females and improved OPVs as male parents in breeding topcross hybrids (IVHs) is being evaluated at ISC. The IVH strategy provides better opportunities for breeding DM-resistant female parents by permitting a much wider option in the choice of female parents of these hybrids, which no longer have to be male-sterile lines. The use of DM-resistant OPVs as pollinators will contribute to the stability of DM resistance and minimize adaptation problems of these IVHs. A small proportion of seeds in the hybrid seed lot will obviously be the sibs from the female parent. The IVHs will be less uniform than those based on male-sterile lines. However, under the prevailing agricultural situations in western Africa, less uniformity of IVHs is unlikely to be a barrier in their acceptance. An additional advantage of IVHs compared to hybrids based on male-sterile lines is that they can be expected to be more prolific pollen producers, which is likely to reduce the incidence of smut and ergot on these hybrids.

Preliminary results of 4 different trials (each consisting of 4-8 IVHs and their respective OPV pollen parents), evaluated at 2-4 locations in western Africa in 1992, showed IVHs having 14-54% higher grain yields than their respective OPV pollen parents. IVHs were also less DM-susceptible than their respective OPV parents. Twelve out of 28 hybrids from these trials have been selected for further multilocational evaluation during 1993. ISC, in collaboration with NARS in western Africa, has also started investigations into (i) procedures for hybrid seed production in isolations, (ii) proportion of sibbed seed in the hybrid seed lot and its effect on hybrid grain yield, (iii) loss in grain yields of advanced generations of IVHs, and (iv) response of IVHs to improved management. Three-way hybrids, based on crosses between male-sterile F_1s and inbred restorer lines, may also combine many of the advantageous features of the topcross hybrids mentioned above. The use of F_1s rather than inbreds as seed parents may also contribute to reducing the cost of hybrid seed and increasing the life span of disease resistance of seed parents, which otherwise frequently break down to DM. Male-sterile F_1s outyield their higher-yielding parental lines by 30-108% and are generally as resistant to DM as their more resistant parents (Rai et al., 1991). The phenotypic variability with three-way hybrids, as theoretically expected, is generally more than within single-cross hybrids but much less than within OPVs.

6. Collaboration with NARS and Networks

Pearl millet improvement activities in all of ICRISAT's regional programs are conducted in close cooperation with NARSs. For instance, IAC has (i) contributed a large number of OPVs, hybrids, male-sterile lines, and restorers to various trials and nurseries of AICPMIP, and provided segregating breeding materials and hybrid parents to the pearl millet improvement programs of both public and private sector organizations in India, and (ii) conducted various trials and nurseries coordinated by AICPMIP. At present, there are nine ICRISAT-ICAR collaborative research projects on pearl millet, that involve partnership with the AICPMIP Unit and 11 other research institutes/universities of India in addressing as diverse issues as gene pool formation and breeding of OPVs and hybrid parents. The collaborative research effort between IAC and Rajasthan Agricultural University led to the development of an OPV (RCB-IC 9) that was released in 1991 for cultivation in the state of Rajasthan. Nineteen more OPVs and two hybrids that have been jointly bred by IAC and Indian NARSs are currently in AICPMIP trials. The collaborating institutions involve: Rajasthan Agricultural University (6 OPVs); Central Arid Zone Research Institute, Jodhpur, Rajasthan (5 OPVs); College of Agriculture, Gwalior, Madhya Pradesh (3 OPVs); College of Agriculture, Gwalior, and Chandrashekhar Azad University of Agriculture and Technology, Kanpur, Uttar Pradesh (3 OPVs); and Punjab Agricultural University, Ludhiana, Punjab, and National Agriculture Research Project, Aurangabad, Maharashtra (1 OPV each). Of the two hybrids, one has been developed in collaboration with Punjab Agricultural University, Ludhiana, Punjab, and the other one in collaboration with the College of Agriculture, Gwalior. Collaboration with other Asian countries interested in pearl millet is done through the Cereals and Legumes Asia Network (CLAN) that was formed in 1992. Prior to the formation of this network, seed parents, pollinators, hybrids, and OPVs were supplied to workers in South Korea. Two forage hybrids bred on 81A, which are resistant to black streaked dwarf virus, are soon to be released there (B.H. Choi, personal communication).

The Regional Pearl Millet Improvement Workshop of 1988, organized by ICRISAT in collaboration with the Institute for Agriculture, Ahmadou Bello University, Zaria, Nigeria, recommended the establishment of a West and Central African Millet Research Network (WCAMRN) to strengthen NARS research capability in the region. Established in 1990, this network includes 13 countries, ICRISAT, and SAFGRAD. The principal objectives of this network are as follows.

- Develop and reinforce cooperation between pearl millet improvement programs in national, regional, and international institutions.
- Define a set of common objectives and strategies for interdisciplinary research.
- Disseminate information, organize meetings and workshops, and
- Promote better use of human, material and financial resources available to member NARSs to permit transfer of improved technologies to the farmers.

The Swiss Development Cooperation provides funding for the WCAMRN activities. Funds are transferred through ICRISAT for which a Memorandum of Understanding was signed between ICRISAT and the Swiss Development Cooperation. Representatives of the member countries reviewed the constraints to millet production in their respective countries and outlined four projects (Table 6) for implementation. ICRISAT provides technical and administrative back up to these approved network projects, which emphasize transfer of improved technologies to the farmers by NARSs.

ICRISAT's pearl millet research in the eastern Africa is a minor activity and it is implemented collaboratively through the Eastern Africa Regional Sorghum and Millet (EARSAM) Network that was established at Nairobi, Kenya in 1986. At present, this activity relates to the evaluation of productivity and adaptation of experimental cultivars developed at IAC and the other two regional programs in Africa. SADC/ICRISAT in the southern Africa does not have a formal network. The SMIP of SADC/ICRISAT, however, functions as a nucleus of a community of 10 nations in the region. Instead of developing common research agenda involving these countries on the issues of regional significance, SMIP follows the strategy of assisting NARS in developing their research capability for their own individual breeding programs. This has involved a strong training program for NARS scientists and technicians, on their own experimental stations, at SADC/ICRISAT Center, and in collaboration with the International Sorghum/Millet Collaborative Research Support Program (INTSORMIL) of the USA. SMIP also conducts collaborative research with each of these individual country programs.

Table 6. Summary of projects of the West and Central African Millet Research Network (WCAMRN).

Project	Participating country	Expected result
Project 1 Extension and adoption of early and/or tolerant varieties to farmers	Burkina Faso, Cameroun, Côte d'Ivoire, Mauritania, Niger, Nigeria*	• Adapted and improved drought-resistant varieties • Availability of seed of improved varieties • Increased millet production • Skills in improved millet production techniques by farmers
Project 2 Improved integrated control techniques for millet earhead insect pests	Benin, Gambia, Ghana, Guinea-Bissau, Mali*, Nigeria, Togo	• Understanding bio-ecology • Development of productive and resistant varieties • Improvement of existing control methods • Development of new and adapted control techniques • Information exchange between NARS, regional and international programs • Improvement in the level of training • Information exchange between farmers, extension workers, and scientists
Project 3 Improved control of downy mildew disease	Burkina Faso, Ghana, Mali, Niger, Nigeria, Senegal*	• Obtain sources of downy mildew resistance • Extension of cultural and chemical control methods accessible to farmers • Heritability of resistance • Increased participation of scientists in regional trials
Project 4 Improved millet-based production systems	Burkina Faso, Côte d'Ivoire, Chad, Mali, Niger*, Senegal	• Maintenance and improvement of soil fertility • Improved management of resources • Improved technical competence of extension agents and farmers

* Lead country for the Project

7. Summary and Conclusions

Pearl millet will continue to be an important cereal crop in the arid and semi-arid tropical regions of Africa and the Indian subcontinent. In the drier and low-resource agricultural situations in these regions, where other sister crops such as sorghum and corn can not be grown or often fail, pearl millet will produce grain, but yields are low. ICRISAT's mandate on pearl millet is to increase and stabilize its grain production through improved technologies developed in partnership with NARSs and in collaboration with other IARCs and mentor institutes.

In a crop improvement perspective, considerable progress has been made (i) in collection, evaluation, and documentation of diverse germplasm, (ii) in developing a better understanding of the nature of several of the major production constraints, (iii) in developing screening techniques to identify sources of resistance to several biotic and abiotic stress factors, and (iv) in utilizing a diverse range of germplasm in developing improved genetic material, including open-pollinated cultivars (OPVs) and hybrid parents.

High-yielding OPVs and hybrids of pearl millet developed at IAC, and hybrids developed by Indian NARS (both public and private) involving IAC-bred hybrid parents, now occupy about one-third (3.5 million ha) of the total area of about 11 million ha planted to pearl millet in India (Ryan, 1992). The IAC-bred OPVs have also performed well and made an impact in parts of southern Africa. Indications are that IAC-bred cultivars will perform equally well in eastern Africa also. IAC-bred cultivars have, however, been found to be unadapted to western African region, which is characterized by a wide range of harsh environment and pest-pathogen complexes. Several high-yielding OPVs bred at ISC, in partnership with NARSs, have reached the farmers' fields and many more are in the pipeline. Currently the impact of these cultivars in the western Africa is limited due to the lack of adequate seed production and/or extension services.

The pearl millet improvement programs worldwide so far have touched only a tiny fraction of the vast germplasm at their disposal. The useful variability identified and generated, and the progress made to date shows no indication of any ceiling having been reached in the genetic improvement of this crop. The great wealth of untapped genetic variability available in cultivated landraces and their wild relatives is, in itself, a good basis for optimism about opportunities for sustained genetic improvement in grain yield and adaptation. With recent developments having enhanced the capability of Indian NARS for applied and adaptive pearl millet research, IAC is gradually shifting its emphasis to more basic and strategic research. Considering that pearl millet research capabilities of NARSs in all the African regions are still inadequate, however, ICRISAT's regional programs and teams in these regions will continue to concentrate on applied and adaptive research. The emphasis in all ICRISAT's pearl millet research programs will continue to be on various aspects related to the genetic improvement, primarily of grain yield and DM resistance. Stover yield will have its own place in the overall crop improvement strategy for those target areas where it is as important a product as the grain yield itself. For drought tolerance, improved plant stand, and resistance to insect pests and *Striga*, the effectiveness of existing screening techniques or those likely to be developed in the future will have to be demonstrated and sources of usable resistance will have to be identified before the genetic improvement for these traits becomes an integral part of the breeding programs.

An increasing use of biotechnological tools will be made in the characterization and mobilization of genetic variability. Plans are underway for enhancing the levels of integration not only amongst various disciplines related to pearl millet improvement but also involving those related to resource management to achieve the goal of increased productivity on a sustainable basis. Besides being a nutritionally excellent coarse-grain cereal for food, pearl millet has a great potential of developing into an excellent feed and forage crop (Andrews and Anand Kumar, 1992). The available genetic resources should lead to genetic gains for feed and forage attributes on par to those for food. Pearl millet may also provide new opportunities for bringing under economic cultivation some of the degraded lands and those with problem soils. The potential of pearl millet for cultivation under intensive agricultural systems (i.e., high input agriculture and high cropping intensity) and as a replacement crop in non-traditional areas has not yet been well assessed and requires future research attention.

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