

Genetic Improvement of Pearl Millet in India

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Abstract Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is grown widely in the arid and semi-arid tropical regions in Indian subcontinent and African continent under the most adverse agro-climatic conditions where other crops like sorghum and maize fail to produce economic yields. Its grains are valued as human food while its dry stover makes important livestock ration in crop–livestock farming system. Enormous progress has been made in the genetic improvement of pearl millet in India during last several decades. This paper presents an overview of strategies followed in genetic improvement of pearl millet, assesses the impact of this research on crop productivity and presents its future prospects in climate-change scenario for providing food and nutritional security. The genetic improvement programme evolved strongly starting from selection in local and traditional material and reaching development of high-yielding hybrids with in-built resistance to diseases and tolerance to climatic stresses like drought and heat. The major approach in hybrid breeding has been to strategically utilize germplasm from Africa and Indian subcontinent with the result that a large number of genetically diverse hybrids have been developed with different combinations of phenotypic traits that are important for adaptation to different ecological regions. The genetic diversification of hybrids has proved very critical to contain downy mildew epidemics which had threatened hybrid technology per se in mid-1970s. A great deal of work has been done on understanding the epidemiology of different diseases and crop response to moisture stress that helped in developing disease-resistant and stress-tolerant cultivars. More than 100 cultivars with a combination of diverse phenotypic traits have been released in the last 25 years, providing a wide range of choice to farmers in different production ecologies of the crop. These cultivars have been widely adopted by Indian farmers with the result that the crop productivity has gone up from 305 kg ha⁻¹ during 1951–1955 to 998 kg ha⁻¹ during 2008–2012, registering a 227 % improvement which assumes greater significance given that more than 90 % of pearl millet is grown as rainfed and often on marginal lands. In future, pearl millet is likely to play a greater role in providing food and nutritional security. Pearl millet would also be an excellent genomic resource for isolation of candidate genes responsible for tolerance to climatic and edaphic stresses for accelerating further genetic improvement of this crop as well as for their possible deployment in the genetic improvement of other crops.

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Introduction

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is a C₄ plant having a very high photosynthetic efficiency and dry matter production capacity. It is usually grown under the most adverse agro-climatic conditions where other crops like sorghum and maize fail to produce economic yields. Besides, pearl millet has a remarkable ability to respond to favourable

environments because of its short developmental stages and capacity for high growth rate, thus making it an excellent crop for short growing seasons under improved crop management.

Pearl millet is cultivated on about 30 million ha in more than 30 countries of five continents viz., Asia, Africa, North America, South America and Australia. Though the majority of crop area is in Asia (>10 million ha) and Africa (about 18 million ha), pearl millet cultivation is being expanded in some of the non-traditional areas, with Brazil having the largest area (about 2 million ha). It is also being experimented as a grain and forage crop in the USA, Canada, Mexico, the West Asia and North Africa (WANA), and Central Asia.

In India, pearl millet is the third most widely cultivated food crop after rice and wheat. It is grown on 9 million ha with an average productivity of 1,000 kg ha⁻¹. The major pearl millet growing states are Rajasthan, Maharashtra, Gujarat, Uttar Pradesh and Haryana which account for more than 90 % of pearl millet acreage in the country (Fig. 1). Most of pearl millet in India is grown in rainy (*kharij*) season (June–September). It is also being increasingly cultivated during the summer season (February–May) in parts of Gujarat, Rajasthan and Uttar Pradesh; and during the post-rainy (*rabi*) season (November–February) at a small scale in Maharashtra and Gujarat.

Pearl millet is primarily grown for food and dry fodder. Its grains are highly nutritious with high levels of metabolizable energy and protein, have high densities of iron and zinc, and more balanced amino acid profile than maize or sorghum [83]. Grains are mainly used for human consumption in the form of diverse food, mostly as leavened and unleavened flat breads and porridges. Dry stover of pearl millet is a major component of livestock ration during the dry period of year [53]. Pearl millet is also an excellent forage crop because of its lower hydrocyanic acid content than sorghum. Its green fodder is rich in protein, calcium, phosphorous and other minerals with oxalic acid within safe limits. A significant portion of pearl millet grain is also used for non-food purposes such as poultry feed, cattle feed and alcohol extraction [11].

During the last more than five decades enormous progress has been made in the genetic improvement of pearl millet, and it is often referred to as a success story in Indian agriculture. This paper presents an overview of strategies and approaches followed in genetic improvement of pearl millet in India. The impact of this research is then assessed on crop productivity. Finally, we also present future prospects of pearl millet in climate-change scenario and in providing nutritional security.

Population Improvement and OPV Development

The genetic improvement of pearl millet in India started in 1930s and largely concentrated on improving the yield by

mass selection and progeny testing, which led to development of some open-pollinated varieties (OPVs). For instance, mass selection in locally adapted material led to the development of C1, C2, Co.2 and Co.3 in Tamil Nadu; T5, T55, A1/3, S350 and S530 in Punjab; AKP1, AKP2 and AKP3 in Andhra Pradesh; Baroda 5, B117, B119 and 14D in Madhya Pradesh; RSJ, RSK, Bari N207 and S14 in Rajasthan; LM 38-39, Bajra 1, Bajra 2, S-14, S 28-25-2, Puri, and Sadas 11 in Maharashtra; and Bijapur 11-11-7-14-6, Golagiri 1-8-5-5 and Sindagi 3-16-13-9-4 in Karnataka [1, 59, 73]. Similarly, improvement for morphological uniformity in a landrace from Ghana at the Indian Agricultural Research Institute, New Delhi led to the development of ‘Improved Ghana’ [52] and further mass selection in ‘Improved Ghana’ led to the development of Pusa Moti [1]. Since these OPVs were developed from landraces with a narrow genetic base and limited field testing, they provided limited improvement in actual yields. Also, these were not backed with adequate seed production, and hence could not make much impact.

The greatest push for the development of OPVs as a part of population improvement programme started in 1970s with the establishment of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). Exploiting a diverse range of germplasm, mostly from the African sources, several composites were developed and improved by recurrent selection, resulting in the development and dissemination of a large number and diverse range of breeding materials. In population improvement programme, various recurrent selection methods (mass selection, gridded-mass selection, recurrent restricted phenotypic selection, S₁ and S₂ progeny selection, half-sib selection and full-sib selection) with varying successes in the genetic improvement of several trait-based composites have been used [34, 36, 88, 101, 140, 160]. A large number of trait-based composites (e.g. early composite, medium composite, late composite, smut-resistant composite, high-tillering composite, bold-seeded composite, dwarf composite and high head volume composite) of broad genetic base were developed till late 1980s [75]. Many of these were improved by recurrent selection and several OPVs were developed. WC-C75, ICMV 221, ICTP 8203, HC 4, Raj 171, JBV 2 and JBV 3, HC 20, RCB 2, CZP 9802 and Pusa 266 were developed from different cycle products of various trait-based composites [56].

Hybrid Development

Pearl millet being a highly cross-pollinated crop with outcrossing rates being more than 85 % [25] and displaying a high degree of heterosis for grain and stover yields, attempts were made to exploit heterosis in the 1950s

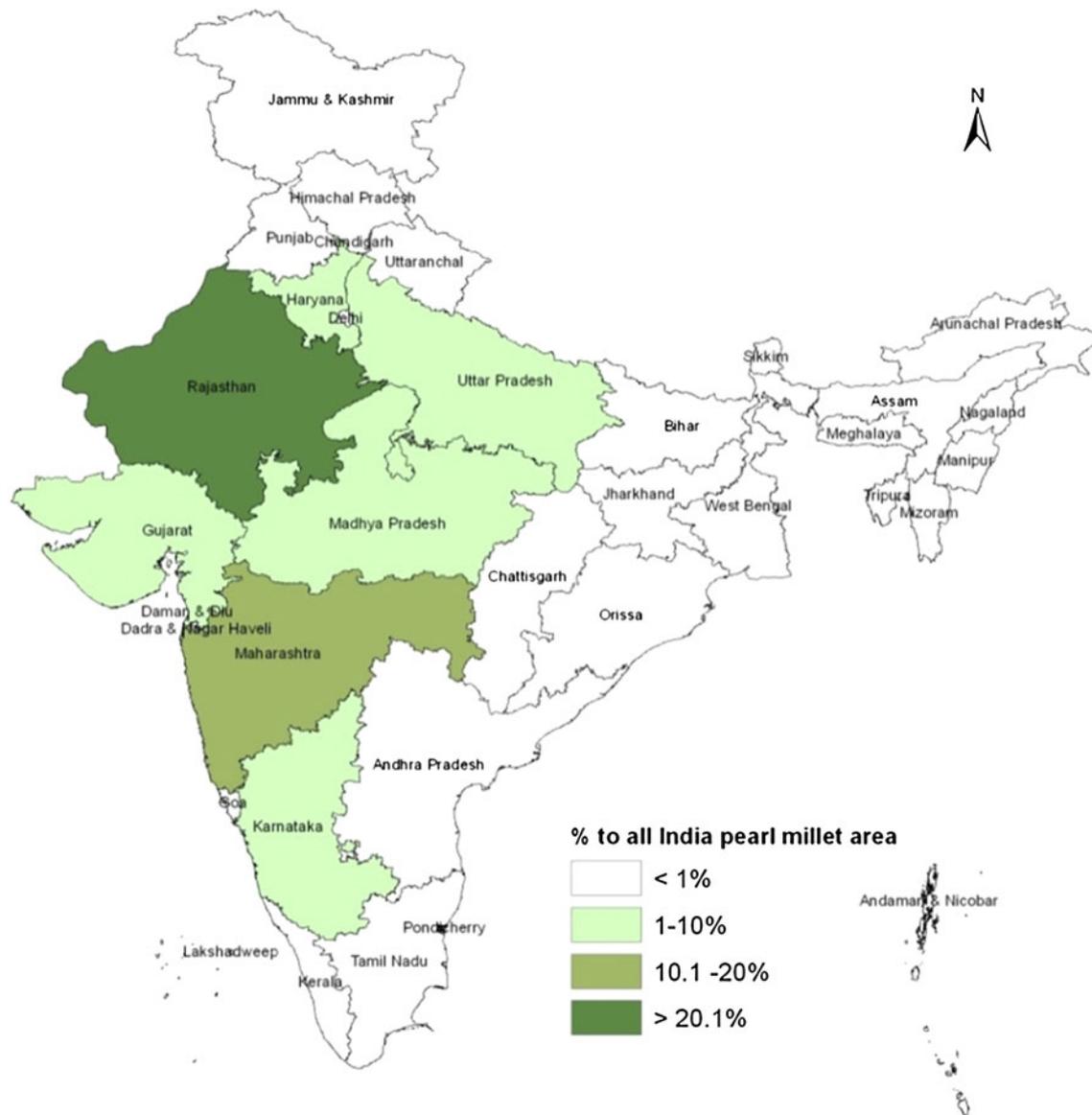


Fig. 1 Distribution of pearl millet in India

utilizing the protogynous nature of flowering of this crop. The usual method at that time for production of hybrid seeds was growing the parental lines in mixture and allowing them to cross-pollinate [34]. The resultant seed contained approximately 40 % hybrid seed when the two parental lines had synchronous flowering at about same time. These chance hybrids thus produced outyielded local varieties by 10–15 %. However, they could not become popular due to their limited yield advantage over OPVs, narrow range of adaptation and lack of seed production programmes.

The above-mentioned limitations in the exploitation of heterosis were circumvented with the discovery of cytoplasmic-nuclear male sterility and release of male-sterile lines Tift 23A and Tift 18A in early 1960s at Tifton,

Georgia, USA. These lines were made available to Indian breeding programmes [8, 9]. The male-sterile line Tift 23A was extensively utilized, both at the Punjab Agricultural University and the Indian Agricultural Research Institute, because of its short stature, profuse tillering, uniform flowering and good combining ability [30]. This laid the foundation of pearl millet hybrid breeding in India.

There have been three conspicuous phases in hybrid development in India (Table 1). In pre-hybrid phase (1950–1965), pearl millet improvement largely concentrated, as described above, on the enhancement of yield in locally adapted materials using mass selection and progeny testing, and a good number of OPVs were developed and released. The introduction of landraces from African countries as well as selection within them also yielded a

Table 1 The four phases of pearl millet improvement in India and their most distinguishing features

Phase	Period	Number of hybrids released	Most distinguishing features of each phase
Pre-hybrid	1950–1965	–	Pre-hybrid phase, few open-pollinated varieties and mostly traditional cultivars largely grown
Hybrid phase I	1966–1980	17	Witnessed hybrid development in pearl millet, a few hybrids dominated cultivation, periodic downy mildew epidemics were common
Hybrid phase II	1981–1995	40	A large number of hybrids based on genetically diverse parental lines developed, downy mildew was largely contained
Hybrid phase III	1996–2012	81	A much larger number of highly diverse seed and pollinator parents used in hybrids, targeting niche adaptation in different zones

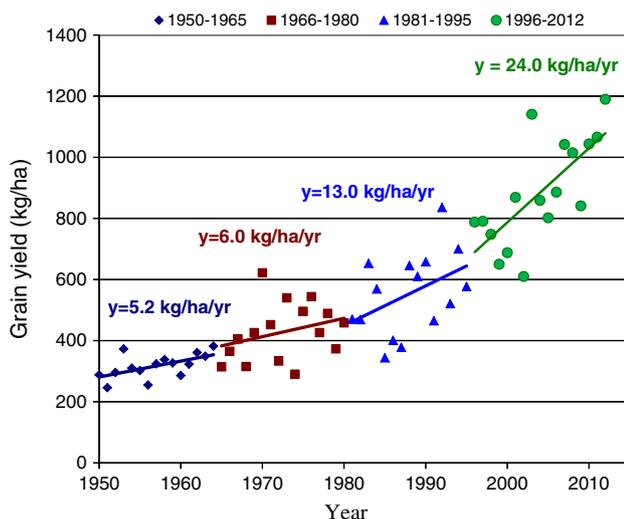


Fig. 2 Trends in pearl millet productivity during 1950–1965, 1966–1980, 1981–1995 and 1996–2012 in India (values inside figure indicate rate of improvement in grain yield in kg/ha/year during each phase)

few useful OPVs for Indian conditions. The average rate of improvement in pearl millet productivity during this phase was only $5.2 \text{ kg ha}^{-1} \text{ year}^{-1}$ (Fig. 2).

Utilization of cytoplasmic-nuclear male-sterile line Tift 23A in the breeding programmes marked the beginning of new phase in pearl millet improvement in India. Tift 23A was widely utilized in hybrid development using pollinators bred in India. As a result, five hybrids (HB 1, HB 2, HB 3, HB 4 and HB 5) based on this line were released between 1965 and 1969. There also existed limited variation in pollinator parents of hybrids [30]. Cultivation of few hybrids with narrow genetic base on large scale led to downy mildew (DM) epidemics offsetting impressive achievements made in hybrid development in the mid 1970s [30]. Thus, there was only modest increase ($6 \text{ kg ha}^{-1} \text{ year}^{-1}$) in pearl millet productivity during 1966–1980 (Fig. 2).

The recurring problem of DM epidemics in pearl millet hybrids till 1980 led to strengthening of research on the diversification of the genetic base of male-sterile lines

(seed parents) of hybrids. As a result, a large number of genetically diverse male-sterile lines were developed and utilized in hybrid breeding during 1981–1995 [55, 56, 71, 155]. Consequently, DM was largely contained and the productivity during this period increased at twice the rate compared to that during the previous phase (Fig. 2).

Current phase (1996 onwards) of hybrid development has put a much greater emphasis on genetic diversification of both seed and pollinator parents. The high productivity with niche adaptation and greater degree of tolerance to diseases are currently being targeted. As a result, rate of improvement in grain productivity has further increased to $24 \text{ kg ha}^{-1} \text{ year}^{-1}$. In the meantime, it was clearly shown that hybrids have 25–30 % grain yield advantage over improved OPVs (Fig. 3). Thus, considering the grain yield advantage of hybrids over OPVs, and the potential for yield gains and production stability (including stemming of any DM epidemics), there was a rapid move away from population improvement and OPV development towards hybrid development.

Research Prioritization

In cognizance of production constraints in and differential requirement of various pearl millet growing regions, prioritization of research has been conceptualized to appropriately address issues that are highly relevant to pearl millet cultivation in specific regions.

Abiotic Constraints

Drought

Pearl millet is most commonly (>90 %) cultivated under rainfed conditions in the arid and semi-arid regions of the country where annual rainfall ranges from 150 to 750 mm, most of which is received during June to September [42]. Because of its cultivation largely in rainfed production systems, pearl millet growth is constrained by several

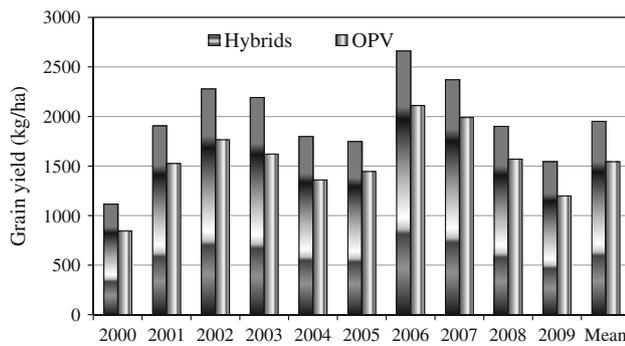


Fig. 3 Average grain yield of pearl millet hybrids and open-pollinated varieties (OPV) evaluated at different locations as a part of coordinated testing during 2000–2009

abiotic stresses. Drought is the primary abiotic constraint and it is caused by low and erratic distribution of rainfall. Hence, research related to the development of pearl millet cultivars suitable for rainfed and unpredictable low-rainfall situations has been a priority area in crop improvement.

A great deal of work has been done on understanding the response of pearl millet to moisture stress at various growth stages that is related to its adaptation to drought stress conditions. It has been conclusively established that effect of water stress depends on the developmental stage during which the crop is subjected to stress. Severe moisture stress during emergence and early seedling phase causes seedling death, which results in poor crop establishment [27, 110] and a significant decline in crop yield. Water stress during vegetative growth may have little adverse effect on grain yield of pearl millet but it has been shown to increase the number of panicles per plant [15, 64]. The apparent excess production of tillers provides potential compensation for damaged main shoot or primary tillers [128, 129]. High tillering and asynchrony of tillering contribute to adaptation to drought stress during the vegetative growth phase [65, 68, 93].

Grain yield losses are highest when stress coincides with flowering and grain filling stages, known as terminal drought stress [61, 63, 65]. Yield reduction is both due to decrease in number of seeds per plant and a decrease in grain mass [15, 33, 64]. The reduction in grain mass is mainly due to shortening of the grain filling period rather than due to a reduction in grain growth rate [20]. Seed setting that determines the number of grains per panicle is usually less affected if terminal stress occurs after flowering [15, 65]. These understandings have helped to prioritize the research in dealing with management of drought stress.

Breeding for increased adaptation to drought has been a challenging task due to various complexities associated with drought adaptation mechanism and uncertainty in timing, intensity and duration of stress. Existence of a large genotype \times environment interaction [54, 126, 127, 132–

134, 145, 148] has indicated that yield performance under drought and non-drought conditions are separate genetic entities, and in situ breeding for drought environments would be required to make greater gains in productivity [15, 33, 125, 146, 152, 153].

Several efforts have been made to identify traits that can be used as selection criteria in breeding drought-tolerant genotypes. Most research has concentrated on the identification of physiological parameters like dehydration tolerance [47], dehydration avoidance [14], growth maintenance through stability of cellular membrane [22], osmotic adjustment [122], desiccation and heat tolerance [112], leaf gas exchange rate [58, 123] and radiation reflectance [14]. However, most of these have hardly found any application in routine breeding programmes, particularly in developing countries, owing to the lack of simple and rapid techniques to select for such characters on a large scale.

On the other hand, morphological characters that can be measured easily appeal most to plant breeders for use as selection criteria. A rapid development of the crop in the initial stages i.e. early vigour has been correlated with drought tolerance as measured by time taken for wilting initiation and permanent wilting in pearl millet [66]. A crop with more rapid leaf area development could intercept a greater portion of incident radiation and limit water losses by soil evaporation. However, there are apprehensions that greater transpiration from a larger leaf area will exhaust soil water resources and cause severe water deficit in later growth stages [139].

Early flowering, the most important factor determining yield under terminal water stress [16, 33], is recognized as another selection criterion, although its advantage is due to drought escape rather than due to drought tolerance. Large genetic variability for earliness is widely available in pearl millet [79, 90] and simple selection has been successful under most circumstances [89]. The most widely used sources of earliness are the *Injadi*-type landraces from western Africa [4, 5]. Early-flowering cultivars bred by using *Injadi* landraces have been widely adopted by farmers in India and Africa.

Panicle threshing percentage or panicle harvest index (PNHI) is another selection criterion proposed for improving tolerance to terminal drought that indicates the plants' ability to set and fill grain under water-limiting conditions and it integrates the effects of assimilation and translocation under water stress. Research has indicated that it usually explains a large proportion of the variation among genotypes for grain yield under terminal drought stress [13, 14, 33]. Results of a selection study on panicle threshing percentage also indicated that grain yield can be increased under stress conditions [13]. Further, it has been shown that even in a small set of inbred lines, the narrow sense heritability for threshing percentage was sufficiently high to expect significant gain

from selection for this trait under drought conditions [143]. Using this selection criterion, an open-pollinated variety (ICMV 221) has been developed from a large-seeded and early-maturing composite.

Low tillering and large panicles are commonly being used as selection criteria in pearl millet breeding. Selecting for these traits results in higher grain yield per panicle [16, 142] which are important yield components in pearl millet [17, 108, 150, 151]. These traits are frequently assessed visually, under both drought and non-drought conditions. However, their specific contribution to improved grain yield and stability under terminal drought condition has not been quantified.

Some studies have also used mathematical models to identify crop cultivars that are productive in stressful marginal environments by comparing the change in seed yield between stress and non-stress (optimum) environments. A drought response index has been developed to provide an indicator of drought tolerance that is independent of escape and yield potential in favourable environments [16]. Drought susceptibility index of pearl millet genotypes is a useful criterion to identify genotypes adapted to drought stress conditions but should be used in combination with yield under stress [146].

Stay-green trait has been widely considered as potentially useful selection criterion for drought tolerance in sorghum [51]. However, its effect, both in the magnitude and the direction, has been shown to be significantly influenced by the genetic background and the environment [51]. Breeding lines with stay-green trait have also been identified in pearl millet, and their multilocational evaluation has been initiated. It would be critical to evaluate the level of expression and stability of this trait in diverse genetic backgrounds before starting its utilization in stay-green breeding programme.

Because of intrinsic difficulties in breeding for drought adaptation [10, 21], this field has become a prime focus for molecular marker-assisted breeding. Genetic mapping for drought tolerance has targeted terminal drought. Several major QTLs have been identified that have significant effects on pearl millet grain and stover yields in terminal drought stress environments [18, 19, 157, 158]. Comparison of hybrids with and without these QTLs showed that QTL-based hybrids were significantly, but modestly, higher yielding in a series of terminal drought stress environments [18]. However, this gain under stress was achieved at the cost of a lower yield under non-drought environments.

One drought tolerance QTL on LG2 [157] has been transferred to drought-sensitive pearl millet lines through marker-assisted backcross breeding [91]. Several introgressed lines carrying drought tolerance QTL from donor parent PRLT 2/89-33 in the LG2 genomic region exhibited

positive general combining ability (GCA) for grain yield under terminal stress, which was associated with a higher PNHI and reduced tillering [159]. Physiological dissection indicated that lines having this QTL had constitutively increased leaf ABA levels and reduced whole-plant transpiration rates as compared to lines not carrying this QTL allele [57].

The genomic regions associated with PNHI were affected both by the genetic backgrounds and the environments (158). Similarly, the effects of stay-green QTL on several physiological parameters related to drought tolerance in sorghum were also significantly influenced by the genetic backgrounds and the environments [124].

Based on the findings mentioned above, it would seem that PNHI and stay-green trait can be targeted as the two morphological features for use in marker-assisted breeding for terminal drought tolerance. However, substantial strategic research would be required to identify major QTL for these traits with stable expression across the genetic backgrounds and the environments before it can be made an integral part of the mainstream breeding programme.

While in recent years there has been a remarkable progress in genomics and genotyping technologies, high-throughput phenotyping became an operational bottleneck. To overcome this, phenotyping is being increasingly automated with the creation of advanced plant phenomics facilities. Advanced imaging systems based on hyperspectral reflectance, visible infrared and near-infrared spectroscopy can capture even small developmental changes in plants in a non-destructive manner. Advances in phenomics, together with genomics and bioinformatics, present exciting new opportunities to understand plant development and adaptation [29]. A phenotyping platform for drought tolerance research using rain-out shelter has been developed at ICRISAT that enables the study of plants ability for water extraction from soil and transpiration efficiency as physiological mechanisms related to terminal drought tolerance.

High Temperature

High temperatures have relevance at both seedling and reproductive stages of pearl millet. The maximum air temperatures around 43 °C are observed in some years in parts of India, especially in the north-western arid zone during the rainy season. The soil surface temperatures during germination may reach 60–62 °C in this zone. Pearl millet seedlings are most vulnerable to high temperatures during the first 10 days of sowing [70, 111]. Rapid screening procedures for seedling survival under these high temperatures have been shown and genotypes with tolerance to high temperature levels have been identified [70, 109]. However, there are no reports of using the identified heat-tolerant

sources in the targeted breeding programme for improved heat tolerance. This could largely be due to the fact that such high temperatures do not occur very frequently and are of restricted geographical distribution to the region with relatively less developed research infrastructure for pearl millet improvement.

There is a growing interest in pearl millet cultivation as irrigated summer season (February–June) crop in parts of Gujarat, Rajasthan and Uttar Pradesh where high temperatures ($>42\text{ }^{\circ}\text{C}$) are of common occurrence during flowering. Such high air temperatures coinciding with flowering in this region can cause spikelet sterility, leading to drastic reductions in grain yield. However, a few hybrids from some of the seed companies (e.g. 86M64 and Proagro 9444), which specifically target this environment for hybrid development, have been found having good seed set and high grain yield of the order of $4\text{--}5\text{ t ha}^{-1}$. The pearl millet area under summer season crop has been on rise and hence expansion of breeding activities related to flowering-period heat tolerance at ICRISAT and in some of the seed companies having field facilities in the target region. As a result of this, large genetic variation for tolerance to heat at reproductive stage among pearl millet breeding lines and populations has been observed, and heat-tolerant lines have been identified. These include several maintainer lines (ICMB 92777, ICMB 05666, ICMB 00333, ICMB 01888, ICMB 02333 and ICMB 03555), improved populations (ICMV 82132, MC 94, ICTP 8202 and MC-Bulk) and germplasm accessions (IP 19799, IP 19877 and IP 19743) [154].

Low Soil Fertility

Soils in the regions where pearl millet is cultivated are often poor in fertility as they contain low amount of organic matter (0.05–0.40 %) because of low vegetation cover, coarse texture of soils and prevailing high temperatures [60]. Soils also contain low-to-medium levels of available phosphorous ($10\text{--}25\text{ kg ha}^{-1}$). This issue has mainly been addressed through nutrient management. Possibilities of genetic enhancement for nutrient-use efficiency have been increasingly being explored in a few crops [45]. Only recently, strategic research at ICRISAT in the Western and Central African region has been initiated to identify QTL for enhanced phosphorous efficiency and to examine the stability of their expression across the genetic backgrounds and the environments.

Biotic Constraints

Pearl millet production is confronted with relatively fewer biotic stresses as compared to other crops. Among the diseases, downy mildew (DM) caused by *Sclerospora*

graminicola (Sacc.) J. Schroet is the most important constraint, especially on those hybrids having DM-susceptible lines in their parentage or when specific hybrid is cultivated continuously in large area. Other diseases include smut caused by *Moesziomyces penicillariae* (Bref.) Vanky, rust caused by *Puccinia substriata* (Ellis & Barth) var. *indica*, blast caused by *Pyricularia grisea* (Cooke) Sacc. and ergot caused by *Claviceps fusiformis* Loveless. Development and application of effective screening techniques; and evaluation of germplasm, breeding material and hybrid parental lines for their reaction to various diseases have been integral components of pearl millet improvement.

Downy Mildew (DM)

DM is the most devastating disease of pearl millet. Grain yield losses due to DM do not usually exceed 20 % but this loss can reach alarmingly higher levels when a single genetically uniform pearl millet cultivar is repeatedly and extensively grown. Cultural and chemical control measures have been worked out but use of resistant cultivars is the most cost-effective control method of DM.

Following good understanding of epidemiology of DM pathogen, highly effective field [136] and green house [98] screening techniques have been developed which easily differentiate between resistant and susceptible progenies (Fig. 4) and are being widely utilized. Screening techniques under green house conditions have been further refined [105] and are highly useful for testing breeding progenies between growing seasons [97].

Several genetic stocks and selections from germplasm accessions and elite breeding materials have shown a high degree of stability for resistance across sites and years [78, 96, 102, 107, 113, 141]. The identified sources of resistance were effectively utilized in developing DM resistant male-sterile lines and pollinators. Moreover, mutation-induced resistance was also successfully utilized. The residual variability for DM resistance could also be exploited to improve the resistance levels of susceptible material. Selection for residual variability for DM resistance in a susceptible landrace population 7042S led to the development of a resistant line which is the most commonly utilized source in DM resistance breeding. Similarly, DM-resistant male-sterile line 841A was reselected from susceptible male-sterile line 5141A [103, 104].

Several putative QTLs have been identified that determine a significant proportion of DM resistance in pearl millet [23, 43, 44, 49, 50]. Resistance alleles at two DM QTLs, one each on linkage groups 1 (LG1) and 4 (LG4), were added to the male parent (H 77/833-2) of one of the most widely grown hybrid, HHB 67 through marker-assisted backcross breeding using a selection from elite parent ICMP 451 as the resistance donor [23]. A more DM-



Fig. 4 Screening for downy mildew using infector-row technique at AICMPIP, Mandor, Jodhpur

resistant version of this early-maturing hybrid was released as ‘HHB 67 Improved’ for drought-prone areas in the states of Rajasthan, Haryana and Gujarat in 2005 [46]. To further enhance the DM resistance level of this hybrid, four new QTL from different donor parents are being transferred to the pollen parent of HHB 67 Improved. Also, attempts are underway to transfer some of the major DMR QTL to ICMB 93333 (seed parent of a released hybrids RHB 127) and J 2340 (pollen parent of popular hybrids GHB 538, GHB 774 and GHB 732).

Smut

Smut, considered as a minor disease, gained considerable importance after widespread cultivation of hybrids. Smut is most severe on the upwind borders of isolated fields especially on the earliest flowering panicles when pollen availability is limited. It can be more serious on hybrids that have more synchronous flowering and/or poor fertility restoration, especially when rainfall and high humidity coincide with flowering, resulting in poor anther dehiscence.

A highly effective screening technique for smut resistance [117] involves inoculation of panicles by injecting aqueous suspension of sporidia into boot, covering the inoculated panicles with parchment paper selfing bags, providing high humidity (>80 % RH), removing bags 2–3 weeks after inoculation and scoring for smut severity.

Significant progress has been made in incorporating smut resistance from unadapted source materials into commercially useful male-sterile lines using pedigree–bulk breeding procedure. ICMA 88006 was the first smut-resistant male-sterile line developed using these methods. Several other smut-resistant male-sterile lines have been bred at ICRISAT. There are conflicting reports as to whether pearl millet reaction to smut is affected by cytoplasm [119, 149] and have been discussed in detail [144]. It is not the A₁ cytoplasm per se but the cytoplasm-mediated male sterility that enhances the susceptibility of A₁ system A-lines and their hybrids to smut [77]. Simply inherited recessive ‘tr’ allele which conditions trichomelessness to

most above-ground plant parts, including stigmas, confers a useful degree of smut resistance [135, 137].

Ergot

The causal fungus of ergot produces both asexual and sexual spores. Sclerotia of fungus are the major source of inoculum and play an important role in perpetuation of ergot. They also contain a neurotoxic alkaloid and the presence of sclerotia in higher number renders the grain unfit for consumption.

Cultural methods of control have been suggested but host plant resistance is considered as the most cost-effective and sustainable control measure for this disease. Field screening technique [115] for ergot disease include bagging of panicles at boot-leaf stage with selfing bags to allow stigma emergence in a pollen-protected environment, inoculating panicles at stigma emergence and briefly opening the bags and spraying the panicles with an aqueous conidial suspension produced from honey dew of infected panicles, providing high humidity (>80 % RH) and removing bags and scoring ergot severity.

Screening of a large number of pearl millet inbred lines at different locations revealed no lines with satisfactory ergot resistance. Resistant lines were developed by intermating plants scored as less susceptible and selecting resistant progenies under high disease pressure for several generations following pedigree and recurrent selection procedures [28, 35, 116]. A number of lines thus developed have shown a high level of resistance across different locations in India and Western Africa over several years [114, 118]. Lines with high levels of resistance combined with good agronomic traits have also been identified and used as donors for developing ergot-resistant varieties. About 300 ergot-resistant inbred lines and populations have been evaluated for their agronomic attributes and reaction to diseases [120]. A number of these lines and populations possess improved agronomic traits and combined resistance to ergot, smut, DM and rust [44].

Attempts were also made to incorporate resistance in the seed parents and pollinators using backcross breeding

procedures [6]. Besides, creating ergot-resistant composites, efforts were made to develop ergot-resistant male-sterile lines to permit hybrid seed production in ergot-prone environments and for possible development of ergot-resistant hybrids. Using pedigree breeding methods, ergot resistance has been incorporated into agronomically elite genetic backgrounds and ergot-resistant male-sterile lines (ICMA 91333, ICMA 91444 and ICMA 91555) have been bred [44].

Inheritance of ergot resistance is relatively complex and may involve cytoplasmic \times nuclear interactions [120, 144]. It has been established that the A_1 cytoplasm per se is not associated with high ergot severity, rather cytoplasm-mediated male sterility is responsible for increased ergot severity of male-sterile lines and their hybrids [76]. Resistance behaves as a recessive trait and it is polygenically controlled.

Rust

Rust of pearl millet is considered as a minor problem because of its late appearance, generally after grain filling stage. However, where the disease is observed as early as seedling stage, it can cause substantial reduction in grain and fodder yield and quality.

Since pearl millet rust has not been considered of great significance, there has not been much research on the development of screening techniques. Materials are generally evaluated under natural conditions with earlier-sown infector rows during the winter season in peninsular India having mild winter.

Several concerted efforts have been made to identify resistance sources for pearl millet rust. A large number of germplasm accessions have been evaluated for their reaction to DM and rust, and many accessions with resistance to these two diseases have been identified [3, 95].

Rust resistance in pearl millet has been demonstrated to be under the control of a single dominant gene [7]. However, gene systems involving polygenes, that impart quantitative inheritance and may lead to horizontal resistance is not ruled out [106]. Pedigree, pedigree–bulk and backcross breeding procedures are used in segregating materials produced from crosses of agronomically elite, rust-susceptible hybrid parents and donors having stable resistance. However, this may not be sufficient to achieve durable resistance in single-cross hybrids for forage purposes [44]. Two QTL have been identified for rust resistance, but their deployment in the parental lines is yet to begin.

Blast

Blast pathogen isolate of pearl millet does not cross-infect rice and finger millet and vice versa. Although it was

considered a minor disease of pearl millet till 1990s, its incidence has increased considerably during the recent years [2, 62].

Breeding for blast resistance had not been as high priority as it has been for DM resistance but stringent monitoring has been a regular feature in national testing system to ensure that no susceptible cultivars were released for cultivation. However, it is now gaining increasing importance due to its high and widespread incidence in India. Field and greenhouse screening techniques have been developed and sources of resistance have been identified [92, 121]. Inheritance studies have indicated major single gene control with resistance being dominant and a single gene effective in imparting resistance [39, 138]. However, three independent dominant genes for blast resistance have also been reported [41]. Three major QTL for blast resistance have been identified. A major foliar blast resistance QTL has been transferred to seed parent of popular hybrid HHB 146. Extensive marker-assisted foreground and background selections are underway to remove negative linkage drag, and retain high levels of blast resistance (Rakesh Srivastava, personal communication).

Cytoplasmic Diversification of Seed Parents (A-Lines)

Discovery of a commercially viable A_1 system of cytoplasmic-genic male sterility (CMS) in 1958 in the USA [24], and its availability led to CMS-based pearl millet hybrid breeding in India. While it still continues to be the only CMS source used in almost all the breeding programmes, concerns with the potential vulnerability of hybrids to diseases and insect-pests associated with the deployment of a single cytoplasmic background spurred research efforts towards identifying and using alternative CMS sources in hybrid breeding. This led to the identification of several alternative CMS sources in India and elsewhere. Some of these were more extensively characterized and classified as different from each other and from the A_1 CMS system. These include A_2 and A_3 [8, 9, 26], A_v [67], A_4 [40] and A_5 CMS systems [74].

Stability of male sterility across the genetic backgrounds and environments is the primary determinant of the commercial viability of a CMS system. Frequency of maintainers in a diverse range of materials and association with traits of economic importance are the other important determinants. Comparative studies using isonuclear A-lines showed that the A_2 and A_3 system A-lines were highly unstable as they had high frequency of pollen shedders, A_v system A-lines were no better than the A_1 system, while A_4 and A_5 systems A-lines were more stable, with A_5 system being the best [80, 81, 84]. It was also observed that the frequency of maintainers was highest for the A_5 CMS system followed by the A_4 and A_1 CMS systems, thus providing greater

opportunities for genetic diversification of A-lines with the A₅ and A₄ CMS systems, in that order, than the A₁ CMS system [84]. This study also showed that while A₅ CMS system had no adverse effect on grain yield, the A₄ CMS system reduced grain yield by about 5 %, as compared to the A₁ CMS system, with large genotypes × environment interaction in these CMS backgrounds. Based on these results, greater use of the A₄ and A₅ CMS systems has been made at ICRISAT for breeding a diverse range of A-lines. Thus, during the last 15 years (1998–2012), ICRISAT developed and disseminated 143 A-lines to the public and private sector breeding programmes, of which 49 are based on A₁ CMS system, 73 on A₄ CMS system and 21 on A₅ CMS system. A recent consultation meeting with hybrid parents users also suggested that greater use should be made of the A₄ and A₅ CMS systems in A-lines breeding [86]. Lack of restorers of the A₄ and A₅ CMS system A-lines, especially of the A₅ CMS system, has been the greatest constraint in their utilization for hybrid development. An efficient breeding strategy for converting A₁ system restorers (otherwise maintainers of the A₄ and A₅ CMS systems) was developed [82] and ICRISAT has initiated a major effort in breeding A₅ system restorers.

Grain Quality

Pearl millet is a highly nutritious cereal with higher levels of proteins and several minerals than other major cereals [99]. Early research showed large variability for protein content, reaching up to 24.3 % in germplasm [48] and up to 19.8 % in breeding lines [100]. However, no serious efforts were made to improve protein content in pearl millet, largely on account of negative correlations reported between protein content and grain yield [99]. Recently, there has been global recognition of widespread deficiencies of iron (Fe) and zinc (Zn), leading to numerous adverse health consequences, especially in the developing countries heavily dependent on the cereal-based diets. Among the 26 major risk factors of the global burden of the disease estimates, Fe deficiency ranks 9th and Zn deficiency ranks 11th [32]. India loses about 4 million disability-adjusted life years (DALYs) annually due to Fe deficiency and another 2.8 million DALYs due to Zn deficiency [72].

Pearl millet accounts for 20–63 % of the total cereal consumption in parts of the major pearl millet growing states such as Rajasthan, Gujarat and Maharashtra [69]. In these areas, it contributes 19–63 % of the total Fe intake and 16–56 % of the total Zn intake from all food sources. Considering the importance of pearl millet in addressing Fe and Zn deficiencies, ICRISAT, with support from the HarvestPlus Challenge Programme of the CGIAR, has initiated a major research thrust on developing improved breeding lines and cultivars with high Fe and Zn density.

A three-pronged approach was followed to (i) assess the variability for Fe and Zn density among the released and commercial cultivars to identify those with high levels of these micronutrients for immediate delivery and up scaling, (ii) exploit the variability for Fe and Zn density within the OPVs to develop their improved versions and to identify hybrids parents with high Fe and Zn density to develop hybrids with high levels of these micronutrients to meet the medium-term objective, and (iii) develop hybrid parents with high levels of Fe and Zn density through targeted breeding for these traits, for eventual use in breeding hybrids with high levels of these micronutrients to meet the long-term objectives. Evaluation of 18 released OPVs showed large variability (43–70 ppm Fe and 36–50 ppm Zn density) with an *iniadi* landrace-based popular OPV (ICTP 8203) having the highest levels of both micronutrients (KN Rai et al., unpublished data.). A similar study of 122 released and commercial hybrids showed 31–62 ppm Fe density and 32–54 ppm Zn density with a highly popular and widely cultivated hybrid (86M86) having the highest level of Fe (60 ppm) and Zn density (50 ppm). Hybrids parents with Fe density exceeding 60 ppm have been identified and are being used to develop high-Fe hybrids in high grain yield backgrounds. Also, breeding lines and germplasm exceeding 100 ppm Fe density and 60 ppm Zn density have been identified [85] that are being validated for use in hybrid breeding.

It has been observed that Fe and Zn densities in pearl millet are largely under additive genetic control [37, 131], implying that population improvement and OPV development for these two micronutrients is likely to be highly effective, and to breed hybrids with high Fe and Zn densities would require breeding both parental lines with high levels of these micronutrients. These studies as well other studies [38, 85, 130] also showed highly significant and positive correlation between Fe and Zn densities, implying that simultaneous selection for these micronutrients is likely to be highly effective. While one study [38] reported no correlation between Fe and Zn density on one hand and grain yield on the other, another study [85] reported negative but weak correlations in a series of trials (though not always significant), warranting further studies on this subject. Further, using a bi-parental RIL mapping population, five major QTL for Fe density and two major QTL for Zn density have been identified and mapped, of which the two QTL for Zn density co-mapped with QTLs for Fe density (Rakesh Srivastava, personal Communication).

Based on the above results, pearl millet biofortification research with respect to Fe and Zn density is gradually being mainstreamed in pearl millet improvement at ICRISAT. Over the years, there has been greater involvement of some of the larger public sector research programmes, and

it is likely to further intensify under the Biofortification Platform Initiative of the Indian Council of Agricultural Research and the mounting evidence that high Fe and Zn density can be combined with high grain yield, and there are standardized rapid and cost-effective techniques available [85] that can enhance the biofortification breeding process.

Trait-Based Breeding

High grain yield combined with high disease resistance and maturity duration, mostly in the range of 75–85 days, as per the agro-ecological requirements has been accorded the highest priority in the cultivar development programme. Due to the growing importance of pearl millet stover for fodder purposes, there has been considerable emphasis in recent times on breeding for high stover yield in combination with high grain yield. Apart from the evident quality traits both in the grain (size, shape and colour) and stover (less rust and blast, thinner stem and lodging resistance) that receive some attention, consideration of any other quality traits in cultivar breeding has been negligible.

Selection for DM resistance has been a top priority in hybrid parental line development. Evaluation of progenies for DM resistance during the course of inbreeding and selection runs concurrent to agronomic evaluation to ensure that B- and R-lines finally produced are resistant to this disease. Trait-specific breeding lines are evaluated for DM resistance against pathotypes from the region for which the lines are targeted. However, breeding lines in some trait-specific groups (e.g. early maturity, medium seed size and average tillering with long panicles) are evaluated in successive steps against more than one diverse pathotypes because of the wider requirements of such materials.

The d_2 dwarf plant height has emerged as the most dominant plant type concept in seed parents breeding. Breeding lines with long panicles (30–80 cm compared to standard normal of 10–20 cm), thick panicles (40–50 mm diameter compared to standard normal of 20–30 mm diameter), and large seed size (17–20 g of 1000-seed mass compared to standard normal of 9–12 g) are currently being developed to breed A-lines with new plant types.

In the breeding of A-lines, high grain yield potential of A-lines, both as lines per se as well as in hybrids (i.e. combining ability), is the most important consideration. High yield, however, is achieved in combination with other agronomic and farmers' preferred traits. Some of the traits in hybrids common to all the environments include lodging resistance, compact panicles and good exertion and good seed set. Traits that have regional preferences include various maturity types, plant height (grain vs. dual-purpose), tillering ability, seed colour and seed size.

There has been a clear distinction between the public and private sector hybrid breeding programmes with respect to trait-based breeding. For instance, private sector breeding programmes have largely focused on relatively better-endowed environments, giving greater emphasis to breeding dual-purpose hybrids. As a result, private sector hybrids are generally taller in height, later in maturity, with longer panicles and less number of effective tillers/plant (AI-CPMIP, unpublished data). In contrast, public sector hybrids are generally shorter in height, early in maturity, with smaller panicles and higher number of effective tillers/plant. Private sector has also placed greater emphasis in breeding large-seeded hybrids. ICRISAT follows trait-based breeding approach to develop a diverse range of materials to meet the above-mentioned diverse needs for various agronomic traits, with high grain yield as a common trait as is the case with all the hybrid breeding programmes. These trait-specific breeding lines and hybrid parents are disseminated to both sectors through constitution of trait-specific trials which are evaluated multilocally every year by public sector breeding programmes under ICAR-ICRISAT Research Partnership Project. Under this project ICRISAT also constitutes and disseminates traits-based trials with respect to other traits such as lodging resistance, compact panicles, bristled panicles, dwarf height and stay-green.

Most of the above-mentioned agronomic traits have high heritability, for which visual selection during generation advance is fairly effective. These traits of the parental lines are expressed in hybrids to varying levels, depending on the corresponding traits in the pollen parents. The A-lines must also have complete and stable male sterility, and B-lines must have profuse pollen production ability across the seasons and sites.

The foremost requirement in the restorer lines is its ability to produce profuse pollen that remains viable at air temperatures as high as 42–44 °C. Also, pollen parents must produce highly fertile hybrids, which confers some degree of protection from ergot and smut infection. Besides being able to produce high-yielding hybrids, the restorers should also be highly productive, which is important from the viewpoint of seed production economy. It is desirable to breed pollinators of 150–180 cm height, but no shorter than the A-line with built-in attributes of panicle, maturity and tillering that will be preferred by farmers in the hybrids. Pollinators must have acceptable level of lodging resistance and should also possess adequate levels of resistance to various diseases.

Cultivar Development

Two cultivar types are available in pearl millet which includes hybrids and open-pollinated varieties (OPVs). Most

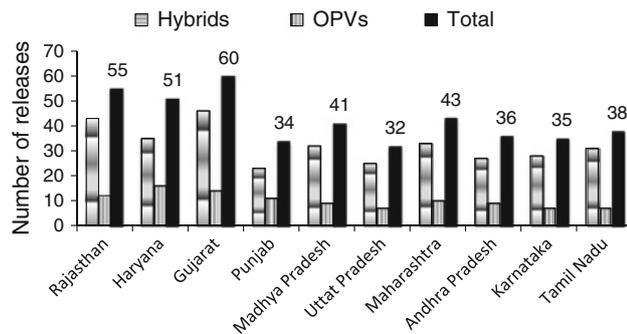


Fig. 5 Number of hybrids, OPVs and total cultivars released and notified for cultivation for different states since 2000

of the breeding programmes are targeted towards hybrids as hybrids generally have 25–30 % grain yield advantage over OPVs [156]. Using diverse male-sterile lines and pollinators, 90 hybrids have been released in the last 25 years by both public and private sectors [155]. In addition, a large number of private sector hybrids are also commercialized as truthfully labelled seed. This has enabled farmers to choose from a wide range of available cultivars (Fig. 5) with appropriate trait combinations that they consider fit to meet their requirement in different crop production environments of various states. In addition, availability and cultivation of a large number of hybrids provides buffering mechanism against diseases, insect-pests and environmental vagaries. Hybrids like HB 1, HB 3, BJ 104, BK 560, MH 179, Pusa 23, GHB 30, HHB 60, HHB 67, MLBH 104, MBH 110, Eknath 301, ICMH 356, Shradha, Saburi, JKBH 26, 7686, 7688, HHB 67 Improved, RHB 121, GHB 538, GHB 558, GK 1004, Proagro 9444 and 86M 64; and OPVs like WC-C75, Raj 171, ICMV 155, ICMV 221, ICTP 8203, CZP 9802 and JBV 2 became very popular with farmers soon after their release.

Cultivar development programme has been very dynamic to cater to changing needs of different regions and sectors as exemplified by three cases. First, when cultivation of hybrids HB 1, HB 3, BJ 104 and BK 560 year after year almost in whole country between 1965 and 1980 created a situation congenial for downy mildew pathogen to proliferate and overcome the disease resistance of individual hybrids, they were withdrawn from cultivation and were replaced with new disease-resistant hybrids viz., MH 179, Pusa 23, MLBH 104, MBH 110 and Eknath 301 [30]. These hybrids were again widely grown after 1980s. Upon succumbing to downy mildew, these were replaced by another series of hybrids like ICMH 356, Shradha, Saburi, JKBH 26, 7686, 7688, HHB 67 Improved, GHB 538, GK 1004, Proagro 9444 and 86M 64. This could become possible due to the strong feeder mechanism in the national programme to continuously evolve DM resistant newer hybrids which could circumvent, to a great extent, the DM threat to pearl millet hybrid technology.

Second, several breeding programmes especially from private sector initially targeted relatively more favourable areas by developing several medium to late maturing hybrids (>85 days) that were responsive to external inputs like additional irrigation and fertilizers. As a result, a much wider choice of cultivars was available for such better-endowed areas. On the other hand, stress-prone arid regions faced several environmental, research and infrastructure, marketing and policy constraints [153]. Consequently, the choice of cultivars for drought-prone environments of north-western India was more limited as compared to other zones. The All India Coordinated Pearl Millet Improvement Project (AICPMIP) carved out of A zone (northern and northwestern India) a special zone for pearl millet testing and evaluation for arid zone environments to include drought-prone areas receiving <400 mm of annual rainfall in the adjoining states of Rajasthan, Gujarat and Haryana, which has been termed as A₁ zone. This has comprehensively strengthened the cultivar development programme for drought-prone regions [153].

Third, much greater emphasis was placed till 1990s on development of hybrids with high grain yield. Given the enhanced demand of dairy products in future and ultimately of dry fodder to sustain livestock, pearl millet improvement programme in India has initiated putting more concerted efforts to develop dual-purpose cultivars, meeting the need of both grain and stover [147] to better cater to the need of crop-livestock farming system.

Synergizing Cultivar Development and Production Technologies

Agronomic research conducted both at research station and on farms, led to the detailed recommendations for individual pearl millet growing zone in order to harness the yield potential of cultivars. It has been reviewed previously [12, 31, 87, 94] and is beyond the scope of this paper to comprehensively review the research work on development of production technologies.

Pearl millet crop production research, as practiced in the semi-arid tropical regions, can be divided in two broad areas: (1) intensive management in areas where moisture is generally adequate and (2) low-input management in areas where moisture is the major production constraint. Intensive management includes, among other things, higher plant population (1,75,000–2,00,000 plants ha⁻¹). However, a lower plant population of 1,20,000 ha⁻¹ with wider spacing has been recommended for drier zones with low and erratic rainfall pattern. Response to applied nitrogen fertilizer as high as 90–140 kg ha⁻¹ has been reported from experimental trials in relatively high rainfall areas but farmer recommendations are in the range of generally

40–80 kg ha⁻¹ in various agro-climatic zones. Though weed management by chemical means has been standardized, it has found little application on farmers' fields.

Agronomic research for low-input arid areas has focused on cropping system including legumes and on moisture conservation techniques. Most suitable cropping systems have been worked out for diverse agro-ecoregions [87]. Conservation of moisture through various techniques forms an important recommendation in dry regions growing pearl millet. These techniques include widely spaced crop and use of mulching, both through manipulating topsoil or organic means. However, adoption of agronomic research is mainly confined to better rainfall/supplemental irrigated areas and is always accompanied by the use of improved varieties. There exists a considerable potential for further adoption of modern inputs mainly nitrogen fertilizer in drier areas. Demonstrations of improved cultivars and production technologies have established that pearl millet yields at farm levels can easily be enhanced by 20–25 % by adopting suitable agro-techniques [155].

Adoption of Improved Technologies and Impact

The high-yielding hybrids and OPVs have been widely adopted by Indian farmers. Several factors have contributed to large-scale adoption of hybrids in India: (1) availability of hybrids in the broad maturity duration (60–90 days), (2) recovery of seed cost by farmers with even as low as 10 % higher grain yield with improved cultivars, (3) profitable seed production, distribution and marketing, and (4) a highly developed seed sector and effective contractual hybrid seed production system that has been evolved in India, leading to quality seed production and its timely delivery. The area under improved cultivars has increased considerably over years. Currently, nearly 65 % of pearl millet area is annually planted using more than 80 hybrids and a few improved OPVs, the relative share of public and private sector hybrids being 25 and 75 %, respectively. The adoption level of high-yielding cultivars, however, has been different in various states. The highest levels of adoption are in the states of Haryana and Gujarat (>90 %) while it is lowest in Rajasthan (30 %).

Following the adoption of high-yielding and disease-resistant cultivars (mostly hybrids) and crop production technology, pearl millet productivity has been consistently increasing (Fig. 6). During the last 60 years, the productivity has gone up from 305 kg ha⁻¹ during 1951–1955 to 998 kg ha⁻¹ during 2008–2012, registering 227 % improvement. This productivity increase in pearl millet assumes greater significance in two ways. First, more than 90 % of pearl millet is grown as rainfed and often on marginal

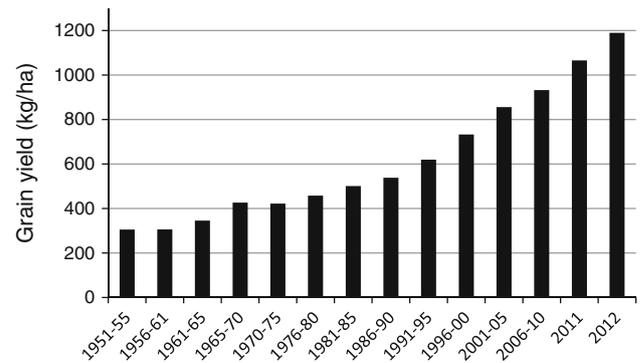


Fig. 6 Productivity of pearl millet in India during 1951–2012 (Source: DAC, Government of India as on 22 July 2013 available at <http://www.agricoop.nic.in>)

lands. Second, pearl millet has attracted much lesser investment in infrastructure and human resources development in comparison to other major food crops. Despite this, the magnitude of yield improvement in pearl millet under rainfed conditions is a successful demonstration of technology-led development and it highlights greatly the role of hybrid technology in raising crop productivity even in marginal drylands.

Future Prospects

The continuing genetic gains of over 24 kg ha⁻¹ year⁻¹ for grain yield, the most impressive in the last decade, indicate that with the greater use of the hybrid technology, employing modern tools, wider inter-institutional and inter-sectoral participation, and improved crop management practices, this productivity momentum not only can be maintained but can even be further accelerated. Although the national productivity of pearl millet is about a ton/ha in the rainy season, adoption of hybrids and improved crop management in the summer season have demonstrated 4–5 tons ha⁻¹ of grain yield in 85 days of crop, indicating enormous yield potential and management responsiveness of pearl millet. The availability of extra-early-maturing cultivars with tolerance to multiple environmental constraints makes pearl millet an ideal cereal for multiple cropping.

The increasing urbanization and industrialization will put heavy pressure on water resources for agricultural use. Further, the climate change will also lead to variable water scarcity. It will also lead to increase in air and edaphic temperatures and soil salinity. Pearl millet being the most water use efficient major cereal under water-limiting environments is also the most heat-tolerant cereal. It is also the most salinity-tolerant cereal next only to barley. These attributes of pearl millet put it in a unique advantageous position to address the multiple environmental challenges, which are likely to be of increasingly serious proportion in

the future. Further, the outbreeding nature of the crop and its evolution under the diverse and challenging agro-climatic conditions has led to large variability, both among and within the populations, which provides great prospects of further genetic improvement.

Recent growth and future projections of aggregate food demand patterns suggest that there will be substantial increase in the demand for animal products (meat, milk and eggs) in India by 2050. Current supply and projected demand of dry stover indicate a 23 % deficit. Pearl millet, being a C₄ species with high photosynthetic potential and biomass production ability, has a greater role to play in arid and drier semi-arid regions to bridge the gap between demand and supply of dry fodder which is the main maintenance ration in dry periods. Pearl millet grain is also being viewed as a potential source to supplement maize supply in poultry and cattle feed industry.

Pearl millet is highly nutritious with high dietary fibre, protein and fat, balanced amino acid profile, and high levels of micronutrients (especially iron and zinc), polyphenols and antioxidants, thus making it a promising crop to address both energy and micronutrient malnutrition issues. Large genetic variability has been found, both among and within the populations for most of the traits to develop improved cultivars with higher levels of these micronutrients. Processing technologies and various types of alternative food products and beverages with further enhanced nutritional values have been developed, and shown to have commercialization potential. These need to be pursued further with the food manufacturing and engineering sectors to scale-up at the industrial level. Further, message of pearl millet as a nutri-cereal (rather than coarse-grain cereal) and health food needs to be promoted not only in the areas where it is traditionally produced and consumed, but also in other areas within India and elsewhere.

Pearl millet is also an excellent genomic resource for isolation of candidate genes responsible for tolerance to climatic and edaphic stresses and their possible deployment in other crops. Sequencing its genome might uncover several genes that might be useful for enhancing the level of stress tolerance in pearl millet and other food crops. Research is underway to sequence representative pearl millet inbred lines, followed by re-sequencing of a large number of pearl millet hybrid parents, germplasm and advance breeding lines. This genome sequence information is likely to significantly accelerate the process of gene discovery and trait mapping, and improve our understanding of the complex gene pathways and interactions.

Developments over the past decade in the field of genomics have provided new tools for faster and precise breeding schemes. Genomics-assisted breeding, whereby selections are made on global marker dataset rather than one or few loci associated with a trait, is becoming a potent

tool to track quantitative traits governed by numerous genes with small effects. With the next-generation sequencing technologies enabling high-density genotyping at relatively lower costs, genomics-assisted breeding is being utilized routinely in many advanced centres for crops like maize [161]. However, in case of pearl millet and other such under-resourced crop species, development of genomics resources is still in embryonic stages. Therefore, the focus in coming years should be to generate a wealth of genomic data and resources for such crops.

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