Pearl millet \([\textit{Pennisetum glaucum} (L.) \textit{R. Br.}]\) is a warm-season, C4 annual cereal primarily grown in Africa and India for food and fodder. It is also grown in the United States, mainly as a forage crop on a limited area. It is the sixth most important cereal crop in the world. More than 90 million people around the world rely on it as a food grain. It is known for its drought and heat tolerance to reliably produce crops in arid environments. This review is meant to assess the current status of pearl millet breeding and its future prospects globally, with major emphasis on breeding efforts in the United States and India. The topics discussed relate to improvements in plant stature, maturity, photoperiod insensitivity, discovery of cytoplasmic male sterility (CMS), and transfer of apomixis from wild relatives. These improvements have led to increased grain and forage yields, nutritional quality, and enhanced disease resistance. Hybrids developed using CMS reportedly have an average of 50% higher grain yield than open-pollinated cultivars. We discuss important genetic and breeding achievements in pearl millet for different traits and their implications for further improvement as a potential crop. Additional research is needed to enhance its productivity, early stand establishment, drought tolerance, and nutritional quality for growing it as a grain crop in moisture-limited areas. The application of advanced genomics and marker-assisted selection tools is needed to accelerate pearl millet breeding and accomplish targeted breeding goals.
nutritional superiority comes from high levels of protein, vitamins, essential amino acids, antioxidants, and essential micronutrients, such as iron and zinc (Agte et al., 1999). Many traditional foods and beverages are made from pearl millet, including couscous, flatbreads, doughs, porridges, gruels, nonalcoholic beverages, and beer. Pearl millet is also a suitable feed ingredient in poultry diets (Davis et al., 2003). Its suitability for poultry diets ensures the bioavailability of micronutrients from its grain for monogastric animals and humans.

Pearl millet is grown as a forage and cover crop on some limited areas in the United States. It has been reported to provide good-quality, high-yielding summer grazing forage (Burton and Fortson, 1966). It has potential as a grain crop for drought-prone areas and poor soil conditions because of its water- and nutrient-use efficiency when compared with other crops, similar to sorghum or maize (Muchow, 1988; Maman et al., 2006). Consumer preferences for gluten-free food products and the demand for millet flour by some African and Asian immigrant communities has been reported to enhance the market for pearl millet grain in the United States (Gulia et al., 2007).

Research on genetic improvement of pearl millet in the United States was started in 1936 at the Georgia Coastal Plain Experiment Station, Tifton, GA (Burton, 1951). The first phase of the pearl millet breeding effort was focused on studying the flowering habit, mode of pollination, and cytogenetics of the crop. These efforts led to the development of inbred lines and improved cultivars (Burton, 1951).

The purpose of this review is to explore and document global pearl millet research efforts and important milestones in its improvement and to discuss their implications for future pearl millet improvement as a grain and forage crop for the drought- and heat-stressed areas, especially in the United States. Breeding achievements for yield improvement, disease resistance, and agronomic performance are reviewed with insights for future research opportunities.

**HISTORICAL PERSPECTIVES OF PEARL MILLET BREEDING**

In the United States, the pioneering pearl millet breeding program initiated by Dr. Glenn W. Burton at Tifton became the foundation for breeding pearl millet elsewhere (Andrews et al., 1993). The program was engaged in fundamental selection and genetic studies for improved cultivar development. Germplasm evaluation and enhancement, genetic studies of agronomically important traits, development of cytoplasmic male sterility (CMS), and identification and utilization of dwarfing genes were important milestones. The first and currently most widely used CMS source (termed $A_1^*_1$) in pearl millet (Burton, 1969), dwarf stocks of early maturity (Burton and Fortson, 1966), and other valuable information on pearl millet breeding and genetics have been disseminated globally from the pearl millet breeding program at Tifton.

The main objective of the US pearl millet breeding program was to develop cultivars for forage purposes. Improvements have been made in biomass productivity and dry matter digestibility by largely using dwarfing genes to increase leaf-to-stem ratio. An in vitro dry matter digestibility study found that digestibility values for pearl millet cultivars were comparable with those for maize but higher than those for sorghum (Ejeta et al., 1987).

Burton’s research also served as the basis for pearl millet grain-hybrid development, mainly in India. Unlike the grain sorghum improvement, pearl millet grain-hybrid development did not begin in the 1960s in the United States (Andrews et al., 1993). This was most likely because of limited research efforts and the emphasis on developing forage cultivars by the pearl millet program in Tifton. In addition, grain sorghum production was already established using dwarf and semidwarf inbred lines that possessed stalk strength sufficient enough for direct combine harvesting (Andrews et al., 1993). Grain sorghum also had a larger germplasm base than pearl millet for use as breeding parents. Pearl millet grain-hybrid development was constrained in the United States because of the emphasis on forage types and the dearth of grain type breeding stocks of pearl millet. Also, the relative nutritional advantage of pearl millet grain compared with sorghum and other cereals was not widely appreciated at that time.

Pearl millet breeding for grain production began at Kansas State University (K-State), Manhattan, KS, in 1969 and was moved to the then Fort Hays Experiment Station, now the Agricultural Research Center–Hays, KS, in 1971 (Christensen et al., 1984). This program was developed with the cooperation of the USDA and Organization for African Union (OAU) Joint Cereals Research Project in Africa (Andrews et al., 1993). The focus of the K-State breeding program was to improve pearl millet traits that were suited to mechanized production of pearl millet grain hybrids; for example, improved stand establishment, fertility restoration to enhance hybrid seed production, and increased lodging resistance through use of dwarfing genes. Cultivars with large seed size and improved emergence from planting depths of $\geq 10$ cm were selected at Hays to overcome stand establishment difficulties (Stegmeier, 1990). Pearl millet germplasms from East and West Africa, India, Tifton, and the USDA-Germplasm Resources Information Network (USDA-GRIN) collections were used as initial breeding sources. A landrace from the Ghana–Togo called Iniati/Koupela (PI 185642) characterized by thick panicle, good combining ability, early maturity, photoperiod insensitivity, and large grain size (12–16 g 1000 seeds$^{-1}$), was used to improve seed size and stand establishment (Andrews et al., 1993). A cultivar
from Uganda, Serere 3A, contributed early maturity, large seed size, and high grain yield potential to numerous inbred lines, especially in the pollinator (R-line) breeding program (Andrews et al., 1993). Tift A, CMS has been used as the basis for developing seed parents (A and B lines) at K-State (Andrews et al., 1993). Several early-maturing, semidwarf seed and pollen-parent lines were developed. The K-State program collaborated with ICRI SAT and International Sorghum and Millet (INTSORMIL) for germplasm exchange (Stegmeier et al., 1987). Seed parents developed at Hays were provided to ICRI SAT and to the Indian national program (Andrews et al., 1993). Some of these lines were used in hybrid breeding in India.

The University of Nebraska–Lincoln initiated a breeding program on grain pearl millet at the High Plains Agricultural Station at Sidney, NE, in 1984 (Andrews et al., 1993). Germplasm introduced from India and Africa by INTSORMIL was used to develop an early-maturing population suited to western Nebraska’s short growing season. Subsequently, adapted seed parents in A1 and A2 (monodii) male-sterile cytoplasm with improved seed yield and lodging resistance were developed for use as grain hybrid parents, and in the development of synthetics for use as open-pollinated cultivars.

The initiation of several pearl millet breeding programs in the United States stimulated the establishment of cooperative pearl millet regional grain yield trials, starting in 1988 (Andrews et al., 1993). Results of experimental hybrids tested at USDA-ARS, Tifton; K-State, Agricultural Research Center–Hays; and University of Nebraska–Lincoln showed that the best pearl millet hybrids averaged 85% of the grain yield of the sorghum hybrids across locations. However, pearl millet yields exceeded sorghum yields in areas with short growing season, and when double-cropped after wheat (Stegmeier, 1990). The establishment of this regional yield trial resulted in identification of two contrasting pearl millet adaptation zones within the United States, the Midwest High Plains, where early-maturing and lodging-resistant cultivars were found to be well suited to the short growing season of the region, and the southeastern United States, where late-maturing, tall, and foliar disease-resistant cultivars were best suited to the long growing season. The identification of this clustering of pearl millet growing regions in the continental United States enabled efficient utilization of germplasm to develop cultivars for the two specific adaptation zones.

On the other hand, India and West African countries are the major growers of pearl millet (FAOSTAT, 2014). A wide adoption of improved cultivars of pearl millet in India that began in the mid-1960s had an important impact on its productivity. With its short crop life cycle, rapid grain filling, and exceptional ability to tolerate drought and heat, pearl millet has been well suited for grain production in arid regions of India. In India, 9 to 10 million ha of pearl millet is grown annually, with an average 9.3 Tg of grain production (AICPMIP, 2017). More than a dozen states of India produce pearl millet as a major crop, some of which are listed here: Rajasthan, Maharashtra, Gujarat, Uttar Pradesh, Haryana, Karnataka, Madhya Pradesh, Tamil Nadu, and Andhra Pradesh (AICPMIP, 2017). In India, >70% of the production area is sown with freshly purchased single-cross hybrid seed (Yadav and Rai, 2013). With an average annual increase in productivity of ~11.1 kg ha<sup>-1</sup> yr<sup>-1</sup> since the 1950s, the Indian national productivity for pearl millet has reached 1141 kg ha<sup>-1</sup> (Kumara et al., 2014).

Pearl millet breeding in India was started in the 1940s by the Indian Council of Agricultural Research (Singh et al., 2014). During the 1940s and 1950s, sporadic varietal improvement efforts for grain yield through mass selection from locally adapted materials were made (Singh et al., 2014). The breeding program was strengthened with the establishment of the All India Coordinated Pearl Millet Improvement Program (AICPMIP) in 1965 (AICPMIP, 2017). The AICPMIP has centers in 13 states of India, with >18 cooperating centers conducting research targeted at enhancing productivity through breeding high-yielding cultivars and developing crop protection technologies and production practices.

The second phase of pearl millet breeding in India was marked with the introduction of CMS line from the United States in the early 1960s. To increase the productivity of pearl millet in India, hybrid development had become the major breeding objective in the 1960s (AICPMIP, 2017). In India, after the official release of the first sorghum hybrid CSH 1 (Coordinated Sorghum Hybrid) for commercial cultivation in 1964 (Pray and Nagarajan, 2009), the first pearl millet hybrid ‘HB-1’ (Hybrid Bajra-1) was released in 1965 (Athwal, 1965a; Pray and Nagarajan, 2009). The release of HB-1 dramatically improved grain yield productivity of the crop in dry and high-temperature areas of India (Singh et al., 2014). The establishment of ICRI SAT at Patancheru, India, in 1972 further stimulated pearl millet breeding program through germplasm collection, characterization, and dissemination to the national program (Upadhyaya et al., 2007).

Downy mildew [Sclerospora graminicola (Sacc.) J. Schrot.] epidemics had become the recurring problem, and most of the hybrids based on Tift 23A<sub>j</sub>, released in India in the 1960s, were pushed out of production shortly after their release (Singh et al., 2014). These downy mildew epidemics required genetic diversification of hybrid seed parents. Then, the third phase of the Indian pearl millet breeding program that started in 1981 was focused on genetic diversification of the CMS seed parents and restorers. Consequently, in addition to conducting strategic breeding, crop management, and value-addition research, AICPMIP also stimulated pearl millet germplasm
collection, conservation, characterization, evaluation, and documentation (Kumara et al., 2014). Field and greenhouse screening of a large number of germplasm from West Africa identified sources of downy mildew resistance (Singh et al., 1997; Thakur et al., 2006). Then, the rapid cultivar turnover because of downy mildew was slowed through transfer of resistance genes from resistant sources (Howarth and Yadav, 2002). This third phase of the pearl millet breeding program also marked the beginning of marker-assisted breeding, and marker-assisted backcrossing played a pivotal role in downy mildew resistance breeding.

The current and fourth phase of the pearl millet breeding program in India that has been running since 1996 is focused on improved genetic diversity of seed and pollinator parents to enhance abiotic stress tolerance and targeting adaptation to specific niches (Govindaraj et al., 2010; Lata, 2015). This fourth phase is marked by the release of the largest number of cultivars and remarkable productivity increase (Kumara et al., 2014). Biofortification of the grain for micronutrients, mainly iron and zinc (Rai et al., 2013; Kanatti et al., 2016a, 2016b), and application of molecular technologies to expedite the cultivar development process were also strengthened. Research aimed at further diversification of the seed and restorer parents, improving disease resistance, and development of extra-early hybrids for adaptation to specific niches is being conducted (Singh et al., 2014).

Development of molecular markers and genetic mapping of pearl millet that was started at ICRISAT also brought a paradigm shift in pearl millet breeding. The first linkage map of pearl millet was constructed using restriction fragment-length polymorphisms in the 1990s (Liu et al., 1994). This trailblazing undertaking for this “orphan crop” provided insights into the genome structure of pearl millet (Serba and Yadav, 2016). As current pearl millet genome sequencing effort by the International Pearl Millet Genome Sequencing Consortium is also led by ICRISAT, the consortium has made reputable contributions in the genetic improvement of the crop.

Although the development of open-pollinated varieties (OPVs) had slowed down in India, it continued to be the primary pearl millet breeding objective in West Africa. Ease and economy of seed production, relatively less vulnerability to biotic and abiotic stresses, and the absence of a viable seed industry are contributing factors towards the preference of OPVs over hybrids in major pearl millet growing areas of Africa (Kumara et al., 2014). Through interpopulation improvement, landraces with thicker stems and longer panicles are predominantly grown for dual purposes (grain and fodder) in West Africa.

Combining ability studies on population hybrids of African landraces reported the prevalence of a high level of heterosis that can potentially contribute to enhancing productivity in the Sahelian and Sudanian environments of West Africa (Ouendeba et al., 1993; Pucher et al., 2016). The current scanty hybrid breeding programs in West Africa are focused on the development of population and topcross hybrids to maintain the intervarietal heterogeneity for higher population buffering potential in stressed environments than genetically uniform single-cross hybrids (Haussmann et al., 2012). As hybrids need optimal growing conditions to perform well, small-scale farmers do not prefer pearl millet single-cross hybrids in the harsh growing conditions of West Africa. It is therefore presumed that development and adoption of population and topcross hybrids would be potentially rewarding in the unpredictable production environments.

**GENETIC DIVERSITY, GERMPLASM COLLECTION, AND ENHANCEMENT**

Genetic diversity is the most important requirement for developing new cultivars with improved yield, quality, and tolerance to biotic and abiotic stresses. Since pearl millet’s domestication ~4500 to 5000 yr ago, natural and human selection processes have resulted in the development of diverse cultivars adapted to different environments, suited to various production systems, and aligned with different consumer preferences (Brunken, 1977). Diverse germplasm from natural genetic variation and breeding stocks created through crossing of diverse germplasm have been used by breeding programs to successfully develop high-yielding and stress-tolerant cultivars. A good example of a high-yielding hybrid with a high level of downy mildew resistance and drought tolerance is the MH 1234 hybrid, recommended for drought-prone areas of India.

Considerable variability exists for various agronomic traits like flowering time, panicle length, grain and stover characteristics, nutritional composition of the grain, and tolerance to biotic and abiotic stresses in the cultivated pearl millet (Bhattacharjee et al., 2007; Amadou et al., 2013). The wide range of climatic conditions in the center of diversity and farmers’ preferences and utilization habits created landraces with local adaptation that maintained broad genetic variability. The prominent early-maturing and productive landrace from West Africa, *inidi*, contributed desirable traits towards genetic improvement of pearl millet (Andrews and Kumar, 1996). The traits contributed by *inidi* include adaptation, productivity, and grain nutritional quality. However, additional information on the genetic control and heritability of the nutritional composition of the grain is needed for effective biofortification of the grain with essential micronutrients.

The study of genetic diversity of *Pennisetum* species recognized three gene pools that were delineated as primary, secondary, and tertiary gene pools (Harlan and De-Wet, 1971). These gene pools were identified for crossing possibility, cross fertility, and gene transfer complexity to cultivated *P. glaucum*. The primary gene pool included...
Natural variability does not always satisfy crop improvement needs of plant breeders regarding agronomic traits, pest resistance, and environmental adaptation. Thus, all forms of cultivated, weedy, and wild diploids \((2n = 2x = 14)\); the secondary pool consisted solely of tetraploid \(P. purpureum\) (Shum.) \((2n = 4x = 28)\); and the tertiary pool included distantly related \(Pennisetum\) species of various ploidy levels (Dujardin and Hanna, 1989a).

There are 1283 active collections of pearl millet accessions maintained at GRIN. More than 75% of these accessions were collected from Zimbabwe, India, Nigeria, and Burkina Faso (Fig. 1). Although the center of diversity for pearl millet is believed to be West Africa (Senegal, Mali, Burkina Faso, and Niger), the number of accessions from this region available at GRIN is negligible. The wild relative, \textit{subsp. monodii}, is also predominantly found in that region. The collection from Zimbabwe was made by ICRISAT in collaboration with IBPGR. A total of 265 accessions obtained from GRIN were grown in 2016 at the Agricultural Research Center–Hays. These accessions showed substantial variability for plant height, photoperiod sensitivity, panicle size, and grain characteristics (Fig. 2). This potential diversity suggests the need for additional germplasm collection from the likely center of diversity.

To broaden the extent of genetic variability available to breeders, ICRISAT embarked on germplasm collection and characterization. By 2007, ICRISAT had collected >20,800 cultivated pearl millet accessions and 750 wild relatives through 76 collection missions in 28 countries (Upadhyaya et al., 2007). Most of these collections were made from the center of diversity (i.e., West and Central Africa). To facilitate identification of potential parents for a genetic improvement program, a core collection of 2094 accessions (\(\sim 10\%\) of the entire collection) was identified on the basis of data on 11 quantitative traits (Bhattacharjee et al., 2007). Then, a mini-core collection comprising 238 accessions (1.1% of the collection) was established from the 2094 core collection accessions, using proportional sampling strategy based on 10 qualitative and 8 quantitative traits (Upadhyaya et al., 2011). This stratified information about the ICRISAT collection warrants a persistent availability of germplasm for further improvement of pearl millet.

**MUTATION BREEDING**

Natural variability does not always satisfy crop improvement needs of plant breeders regarding agronomic traits, pest resistance, and environmental adaptation. Thus,
induced mutations are often used as a means to create additional variability and to identify new alleles (Acquaah, 2007). The use of induced mutations in pearl millet breeding has been limited because of readily available natural genetic variation, and the fact that limited studies have been conducted on chemical rate and efficacy and physical mutagenesis effects on plant and seed characteristics of pearl millet inbred lines. Results from a pioneering study using thermal neutron treatments of $5.67 \times 10^{12}$, $1.14 \times 10^{13}$, and $1.70 \times 10^{13}$ (total doses of flux $\times$ time) or 4-h treatments with 0.2, 0.4, and 0.6% ethyl methane sulfonate (EMS) in an unbuffered water solution of air-dried seeds of 10 pearl millet inbred lines showed significant inbred-by-treatment interactions for several traits (Burton and Powell, 1966). They reported changes such as delayed seedling emergence, reduced plant height, delayed maturity, and reduced seed set. Further, they indicated that average chlorophyll-deficient seedling increased with increasing EMS dosage (Burton and Powell, 1966; Burton et al., 1974). These results support the importance of mutation breeding to identify needed traits like dwarfing genes for reducing plant stature.

Ethidium bromide (Burton and Hanna, 1976), streptomycin (STY), and mitomycin (MIT) (Burton and Hanna, 1982) were used as mutagens to induce CMS mutants. Reportedly, the 200- and 500-mg kg$^{-1}$ STY and 50-mg kg$^{-1}$ MIT treatments increased the frequencies of stable CMS mutants by 2.9, 3.6, and 6.2 times, respectively, over the control. Crosses with maintainer and restorer lines indicated that the induced mutants had similar sterility maintainer and fertility-restorer requirements as the $A_1$ cytoplasm, whereas CMS mutants reverted to fertility in the $M_2$ generation (Burton and Hanna, 1976). Viability of pollen irradiated with $\gamma$-rays in the range of 1.2 to 8.0 kR was affected; however, there was enough viability to produce seed, providing an opportunity to recover mutant plants (Hanna and Young, 1974).

A spectrum of mutants with novel traits that cannot be generated with normal genetic recombination can be obtained when homozygous lines are treated with mutagenic agents on a scale that is adequate to create allelic changes. Thus, induced mutation can serve as an alternative approach of generating an array of genotypes, especially for genetic studies and trait mapping in pearl millet. Mutants with reduced plant height, earliness, and CMS has direct practical application in pearl millet breeding.

**PHOTOPERIODISM AND MATURITY DURATION**

Days to maturity and photoperiod are important factors in pearl millet from the standpoint of adaptation, yield, and quality. Almost all pearl millet landraces are photoperiod sensitive and flower in short-day situations (Dave, 1987). Flowering is reduced by long days (Burton, 1965). Photoperiod sensitivity permits flowering and grain maturation at the end of the growing season, despite the planting date. Photoperiod and daylength responses of pearl millet grown in West Africa depend mainly on the latitude of origin of the material (Sanon et al., 2014). Generally, the late-maturing genotypes are short-day types, whereas the early-flowering ones are day neutral (Burton, 1951). Crossing a late-maturing genotype with an early-maturing genotype revealed that photoperiodism in pearl millet was controlled by several genes with additive effects and minimal dominance effects (Burton, 1965).

The early-maturing, inbred-parental lines from the United States are mostly photoperiod insensitive and can flower in the longer daylength of the Great Plains’ summer. This trait allows the pearl millet to escape frost damage that commonly occurs during autumn in the Great Plains by maturing before the frost happens. On the other hand, almost all the germplasm from Africa and India are photoperiod sensitive, and they need to be grown under greenhouse conditions to obtain flowering and grain maturity for breeding programs located in longer daylength areas.

**PLANT HEIGHT AND DWARFING GENES**

The development of dwarf pearl millet cultivars offers potential advantages that include increased lodging resistance, green forage production, and response to inputs. The dwarfing genes have been reported to improve forage nutritive value by reducing stem percentage and increasing leafiness (Burton and Fortson, 1966). There are four recessive dwarfing genes ($d_1$, $d_2$, $d_3$, and $d_4$) in pearl millet that control plant height. Burton and Fortson (1966) found that the $F_1$ of the hybrid between the normal and dwarf genotypes was as tall as the normal inbred parent. The recessive dwarfing gene $d_1$ has been deployed widely in commercial cultivars grown in Australia, India, and the United States (Parvathaneni et al., 2013). Most of the semidwarf parental lines used in the development of US hybrid forage cultivars were developed using the $d_2$ gene (Hanna et al., 1997). The $d_2$ gene reduces the internode length by 50% and, as a result, was reported to do so without affecting the number of leaves (Burton and Fortson, 1966) or the length of the coleoptile and mesocotyl (Soman et al., 1989).

**DEVELOPMENT OF CYTOPLASMIC MALE STERILITY, HYBRID BREEDING, AND POLLEN STORAGE**

Pearl millet is a protogynous species, where the stigma becomes receptive 2 to 3 d before the pollen is released from the same panicle and results in a higher proportion of cross pollination than selfing. Pollination is mainly by wind; insects such as honeybees (Apis mellifera L.) also effect pollination by carrying pollen across long distances.
(Leuck and Burton, 1966). In outcrossing species like pearl millet, exploitation of hybrid vigor could potentially enhance agronomic yield. However, the use of manual emasculation and pollination techniques are labor intensive and cumbersome operations. Thus, heterosis breeding turned to development of male sterility, application of pol lenicides, and other means of suppressing self-pollination.

Pearl millet cultivar development through direct selection from landraces has shown limited success because of narrow genetic variability (Andrews and Kumar, 1996). To improve forage yield, the breeding program at Tifton focused on the development of hybrids. The first four parental inbred lines developed in the Georgia breeding program were named 12, 18, 23, and 26, all of which flowered at the same time. The hybrid combination (seed harvested from the field planted to a mixture of the four selected inbred lines) became the first commercial pearl millet forage cultivar, ‘Gahi-1’, which was released in 1958 (Burton, 1962). The breeder confirmed that this hybrid forage cultivar had >50% yield advantage compared with the check cultivar. This response was observed in clipping and grazing trials, and Gahi-1 reportedly dominated forage yield trials for a number of years (Burton, 1983). The discovery of the $A_1$ CMS system (Burton, 1958) ushered in a new era of pearl millet hybrid cultivar development. All of the forage pearl millet breeding in the United States and most of the grain pearl millet breeding in India switched to the hybrid system (Andrews et al., 1993). This transition to hybrid breeding enhanced both biomass productivity and dry matter digestibility in the United States (Andrews and Kumar, 1992) and grain yield in India (Singh et al., 2014).

The development of the first CMS pearl millet line, Tift 23A, in the United States occurred in 1956 (Burton, 1958). The report indicates that it was inadvertently developed from a cross between Inbred 556 and Inbred 23. Inbred 556 had broad soft leaves and short internodes, produced little pollen, and set little seed when selfed. The cross was made with the objective to increase leafiness in Inbred 23, which is a parent of Georgia Hybrid 1. Half of the selfed $F_2$ plants that resembled Inbred 556 set no seed. The backcross, $(556 \times 23) \times 23$, of the male-sterile $F_2$ 5 was found to shed no pollen and set no seed when selfed, but when dusted with pollen from another source, it readily set seed. The resulting cross demonstrated the characteristics of CMS in pearl millet, and a search for stable maintainers and fertility restorers began as a result of this finding. Initially, crosses were made between the male-sterile plant and 41 inbred lines from diverse germ plasm sources. An evaluation of the $F_5$ hybrids revealed that 27 hybrids were fertility restorers and six had the characteristics of a maintainer line (Burton, 1958). This discovery marked the beginning of hybrid breeding in pearl millet.

The discovery of CMS provided a viable and economical way of producing hybrids and exploiting hybrid vigor in pearl millet breeding programs. A decade after this breakthrough, the first CMS-based forage hybrid, Gahi-3, from a cross between Tift 23DA1 and Tift 186 was released in 1972 (Burton, 1977). This new hybrid yielded 10 to 19% more dry matter and showed 50% higher weight gains in animals that were fed this hybrid compared with those that were fed Gahi 1 (Burton, 1995). Subsequently, the semidwarf TiGrain 102 $(Tift\ 99D2A1 \times Tift\ 454)$ represents the new generation of pearl millet grain hybrids (Hanna et al., 2005a, 2005b). This hybrid had shorter stature, was earlier maturing, had larger grain size, and was easier to combine harvest than previously released cultivars. In addition, it had better resistance to root-knot nematodes ($Meloidogyne$ spp.) and rust ($Puccinia\ substriata$ Ell. & Barth. var. indica Ramachar & Cumm.) than older cultivars. Hybrid seeds of TiGrain 102 became available to farmers on a limited basis beginning in 2002. This new hybrid produced high-quality grain in Georgia, the southern Coastal Plain, and the Great Plains of the United States.

The CMS inbred line Tift 23A$_1$ was introduced in India in 1962 (Burton, 1969). It quickly replaced the hand pollination using protogyny for hybrid production. The seed parent and pollinator parent of HB-1 were Tift 23A$_1$ and Bil 3B, respectively (Athwal, 1965a). HB-1 ($Tift\ 23A_1 \times Bil3B$) yielded, on average, 88% more than the best local cultivars in India and was instrumental in increasing pearl millet grain production from 3.5 Tg in 1965 to 8 Tg in 1970 in India (Burton, 1983).

Subsequently, additional sources of CMS systems that were different from Tift 23A were developed. Two sources of CMS were found in India in a selfed progeny of a cross between an African cultivar and an outcross that had a mixture of yellow and slate-gray seeds. These lines were named '66A' and '67A' and were later designated as $A_3$ and $A_4$ (Athwal, 1965b). Currently, there are five different CMS systems ($A_1$–$A_4$) that are used in pearl millet breeding (Table 1).
disastrous was demonstrated in 1970 by the southern corn leaf blight \textit{Bipolaris maydis} (Nisikado & Miyake) Shoemaker] epidemic. That year, in the US Corn Belt, all of the maize produced with the Texas (T) cytoplasm was found to be susceptible to southern corn leaf blight race T (Scheifele et al., 1970).

Currently, one of the limiting factors in pearl millet breeding is lack of synchronized flowering between male and female parents. This is often the case when the parental inbred lines have marked maturity differences. Staggered planting is practiced in breeding programs to synchronize flowering. However, planting different rows on different days is inconvenient and reduces efficiency of field operations.

Pollen storage provides flexibility and increases breeding efficiency by making pollen available on an as-needed basis. Consequently, the effect of pollen moisture content, storage conditions, and optimal time of pollination on seed set were studied in pearl millet (Cooper and Burton, 1965; Hanna et al., 1983, 1986; Hanna, 1990). Results revealed that pearl millet pollen stored with <8% moisture for 6 mo at −73°C gave 100% seed set when used to pollinate CMS lines (Hanna et al., 1983). A long-term pollen storage study found that pollen with 7% or less moisture content continued to be viable after 1089 d of storage at −73°C (Hanna et al., 1986). In general, <7% moisture content was recommended as the most favorable for maintaining long-term viability of pollen at storage temperatures of −73, −18, and 5°C. Glass vials were found to be more desirable for long-term storage of pollen at −73, −18, and 5°C than plastic Ziploc bags, which reduced pollen viability (Hanna, 1990). The original glassine pollen-collection bags can also be used as storage containers if the pollen is first dried in the bags and the glassine bags are folded and placed in Ziploc bags.

**TABLE 1. Cytoplasmic male sterility (CMS) sources in pearl millet discovered at different times.**

<table>
<thead>
<tr>
<th>Designation</th>
<th>Source</th>
<th>Development place</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>A(_1)</td>
<td>Inbred 556</td>
<td>Tifton, GA</td>
<td>Burton (1958)</td>
</tr>
<tr>
<td>A(_2)</td>
<td>IP 189</td>
<td>Ludhiana, India</td>
<td>Athwal (1965b)</td>
</tr>
<tr>
<td>A(_3)</td>
<td>Amber grain stock</td>
<td>Ludhiana, India</td>
<td>Athwal (1965b)</td>
</tr>
<tr>
<td>ex-Bornu</td>
<td>Gero pearl millet</td>
<td>Ibadan, Nigeria</td>
<td>Aken’Ova and Chheda (1981)</td>
</tr>
<tr>
<td>PT 732A</td>
<td>Subsp. monodii × Tiotande</td>
<td>Gif sur Yvette, France</td>
<td>Appadurai et al. (1982)</td>
</tr>
<tr>
<td>A(_1) (A(_m))</td>
<td>Subsp. monodii</td>
<td>Tifton, GA</td>
<td>Hanna (1989)</td>
</tr>
<tr>
<td>A(_bop)</td>
<td>Genepools</td>
<td>ICRISAT</td>
<td>Sujata et al. (1994)</td>
</tr>
<tr>
<td>A(_3)</td>
<td>Genepools</td>
<td>ICRISAT</td>
<td>Rai (1995)</td>
</tr>
</tbody>
</table>

**BREEDING FOR DISEASE RESISTANCE**

The outright necessity of breeding for stable or durable disease resistance in pearl millet was recognized as soon as the improvement potential of the crop was known. Diseases like downy mildew, rust, and leaf spot became important constraints for pearl millet production with the introduction of hybrids. Epidemiological studies of the major diseases have shown that high relative humidity (85–90%) and moderate temperature (20–30°C) favor infection and disease development (Thakur et al., 2011).

The two most important fungal diseases of pearl millet in the United States are rust and leaf spot (blast), primarily caused by \textit{Pyricularia grisea} (Cke.) Sacc (Wilson and Hanna, 1992). Several other fungal pathogens of minor importance, such as \textit{Cercospora pennisetii} Chupp, \textit{Exserohilum nostratum} (Drechs.) K.J. Leonard & E.G. Suggs, \textit{Drechslera dematioidea} (Bubak & Wroblewski) Subram. & Jain, \textit{Phyllosticta penicil- lae}, and \textit{Bipolaris setariae} (Saw.) Shoem, are also known to cause necrotic leaf spot and foliar blights (Wilson and Gates, 1993). Rust is known to occur to varying extents in areas where the crop is grown (Andrews and Kumar, 1992) and is the most severe disease of pearl millet in the southeastern United States (Wells et al., 1973). Teliospores and uredospores, the asexual spores of rust pathogen, occur on pearl millet and wild grasses, whereas \textit{Solania athiopicum} L. and \textit{Solania melongena} L. are the aecial hosts of this fungus (de Carvalho et al., 2006). The pathogen is primarily disseminated by wind, and the spores can survive in the soil, on plant debris, volunteer pearl millet, and alternative hosts. Rust infection can cause up to 72% yield loss in pearl millet in the southeastern United States (Wilson et al., 1995). A dominant rust resistance gene, \textit{Rr1}, was discovered in three wild grass \textit{(P. glaucum} ssp. \textit{monodii}) accessions from Senegal and was rapidly introgressed into cultivated pearl millet via backcrossing (Hanna et al., 1985). Transfer of this gene to the inbred parents improved rust resistance of the hybrid cultivars. However, this gene was found to be unstable. A single dominant gene controlling vertical resistance in the host can be overcome by a single mutation in the pathogen at the virulence locus or a new race of the pathogen. For this reason, broadening the genetic resistance base or multigene resistance (horizontal resistance) was implemented by combining genes for slow rusting with race-specific resistance in the development of improved forage pollinator lines (Wilson, 2002). Tapsoba and Wilson (1995) evaluated 15 single uredinal isolates of the pathogen on 29 resistant pearl millet germplasm lines. They identified 10 new races based on seedling reaction of the 29 germplasm lines. Their results revealed a definite range of variation in the pathogen population with different level of prevalence. Some of
the germplasm lines were found to be resistant to as many as seven races, indicating that there was non-race-specific (horizontal) resistance present in the germplasm.

Leaf spot of pearl millet, also known as blast disease, is another common fungal disease affecting grain and forage pearl millet production, mainly in the southeastern United States. Blast disease pathogen is characterized by asexual conidia that are pyriform, hyaline, and mostly three-celled, with a small appendage on the base cell that measures approximately 17.5 to 30.8 × 5.9 to 8.8 μm (Mehta et al., 1953). It forms elliptical or diamond-shaped lesions that range from approximately 2.5 to 3.5 mm to 1.5 to 2.5 mm in size on the infected foliage (Hanna and Wilson, 2002). The disease symptoms are gray, water-soaked lesions that turn brown on drying. The lesions are often surrounded by a chlorotic halo that later turns necrotic, giving the appearance of concentric rings. Although progress towards managing various pearl millet fungal diseases has been made, there has been very little accomplished on leaf spot pathogen characterization or management in the United States. Further study of leaf spot disease management practices is still needed. Exploitation of natural genetic variation among germplasm, identification and utilization of new genes for host-plant resistance, precise phenotyping methods, a detailed understanding of pathogen variability, and genetic mechanisms of resistance are areas that need future emphasis for resistance breeding in pearl millet.

Field and greenhouse screening techniques, which involve the establishment of infecter rows of susceptible genotypes as a source of inoculum, pathogen isolation procedures, and severity rating scales, have been developed for downy mildew, rust, blast or leaf spot, ergot (Claviceps fusiformis Loveless), and smut [Moesizomycetes pennisillaricae (Bref. Vanky)] at ICRISAT (Wilson et al., 1989; Singh et al., 1997; Thakur et al., 2011) and are being used in germplasm screening programs elsewhere. Sources of stable resistance to downy mildew and rust have been identified in germplasm from West and East Africa, respectively (Singh, 1990). These materials were strategically used in breeding for resistance at ICRISAT and AICPMIP centers (Wilson et al., 1989; Hash et al., 2006; Thakur et al., 2011). Additionally, remarkable progress towards managing various fungal diseases in pearl millet has been achieved, mainly in India.

However, fungal diseases, especially downy mildew and smut, are still inflicting significant yield losses in major pearl millet-growing areas in West Africa. Farmers are growing disease-resistant but low-yielding landraces to overcome disease epidemics in many parts of Africa. A strategic breeding program that incorporates disease resistance with yield improvement is needed to harness the germplasm available for the development of improved cultivars that are acceptable to the growers.

**INTERSPECIFIC HYBRIDIZATION**

Wild relatives of cultivated species serve as a reservoir of genes that could potentially be used to improve crop cultivars. Accordingly, wild *Pennisetum* species serve as a reserve of germplasm for pearl millet improvement. Thus, there is a great need for systematic collection and preservation of wild *Pennisetum* species for use in genetic improvement of pearl millet (Hanna, 1987). The wild, weedy pearl millet subspecies *monodii* and *stenostachyum* form the primary gene pool for pearl millet improvement. They are the most readily available and easily used wild relatives for crossing with domesticated pearl millet. These subspecies could be used as sources of disease and insect resistance, fertility restoration genes for the A1 cytoplasm, cytoplasmic diversity, and many inflorescence and plant morphological characteristics (National Research Council, 1996).

*Pennisetum purpureum* Schmuck. and *P. squamulatum* Fresen. were effectively used in developing ornamental *Pennisetum* cultivars (Hanna et al., 2010). Two ornamental cultivars of *Pennisetum* were successfully developed by crossing a hybrid of *P. purpureum* and *P. squamulatum* to tetraploid *P. glaucum* (2n = 4x = 28). *Pennisetum purpureum*, known as Napier grass or elephant grass, is a perennial tropical grass native to the African grasslands (Farrell et al., 2002). It thrives well on uncultivated lands with low water and nutrient requirements and is primarily used for grazing in dairy production in the tropics. It has high forage potential, and *P. glaucum* (2n = 2x = 14) × *P. purpureum* (2n = 4x = 28) crossing produces a vigorous, sterile triploid (2n = 3x = 21) hybrid (Jauhar and Hanna, 1998) that may be used in improving pearl millet forage yield and quality. Napier grass has also exhibited potential for use in pull-push pest management strategy for attracting stem borer moths (*Coniesta ignefusalis* Hampson.) away from maize (Khan et al., 2007). This characteristic can also be used in pearl millet production, as stem borer and head minons (*Heliocheilus albipunctella* De Joannis) are the common insect pests.

Interspecific hybridization faces both pre- and postzygotic barriers because of cross incompatibility between species. The success of interspecific hybridization depends on the level of genetic compatibility between the species involved for successful production of interspecific hybrids (Techio et al., 2002). The harmonious function of the genes of the parental species in the development of embryo, maternal tissue, and endosperm that is capable of nourishing the young embryo and the interaction among the three factors are important for viable interspecific hybrid seed development (Fagerlind, 1948). Such compatibility depends on the ploidy-level relationship of the parental species that may result in sterile triploids or pentaploids. The barriers encountered on account of ploidy difference are usually overcome by enhancing the cross
compatibility of the two species using another intermediate species as a bridge (Hanna et al., 2010). In interspecific hybridization, the embryo–rescue technique is commonly applied to overcome postzygotic barriers.

Despite the barriers, several related species were found to be useful in pearl millet improvement. The interspecific hybridization attempts proved the presence of good reservoirs of genes and their transfer for pearl millet improvement. *Pennisetum glaucum* subsp. *monodii* was found to be a source for new CMS, striga (*Striga* spp.), resistance, and rust and leaf spot resistance (Hanna et al., 1985). *Pennisetum purpureum* proved to be a donor of forage yield and quality, stalk strength, and restorer genes of the A1 CMS system (Jauhar and Hanna, 1998). Hybridization with *P. orientale* (Willd.) Rich. can help transfer genes for apomixis, drought tolerance, perennial growth habit, and pest resistance (Hanna and Dujardin, 1982; Dujardin and Hanna, 1987). *Pennisetum squamulatum* has the potential for apomictic gene transfer and *P. schweinfurthii* Pilg. for improved seed size. On the other hand, *P. pedicellatum* Trin. and *P. polystachion* (L.) Schult. have downy mildew resistance, but no hybrid could be formed when they are crossed with diploid and tetraploid *P. glaucum* (Dujardin and Hanna, 1989a).

**APOMIXIS IN PEARL MILLET**

Apomixis is an alternative path of reproduction in plants where an embryo is formed without fertilization and is genetically identical to the mother plant. Apomixis is a form of asexual reproduction where maternal clones are produced through seeds (Nogler, 1984). Apomixis is commonly observed in wild plant species and can be transferred to cultivated species through crossing with apomictic wild relatives, mutation, or genetic transformation (Kandemir and Saygili, 2015). Apomixis occurs in three major forms: adventitious embryony (seeds develop directly from somatic cells, usually nucellar), diplospory (development of a 2n embryo sac from the megaspore mother cell), and apospory (one or more nucellar cells develop into 2n embryo sacs with either seven cells [Hieracium type] or four cells [Panicum type]) (Morgan et al., 1998).

Apomixis is a desirable trait because it can be used to produce true-breeding hybrids, or preserve hybrid vigor regardless of heterozygosity by self-seeding, or enable commercial production of hybrids across generations without CMS (Hanna and Bashaw, 1987). Uniform progenies from heterozygous F1 or open-pollinated parents, maternal-type F3 in crosses, high seed set in unstable genotypes, and multiple ovules and seedlings per ovule are indicators of the presence of apomixis (Hanna and Bashaw, 1987). Successful transfer of apomixis into crop species, which naturally reproduce through sexual means, holds great promise for improving seed production (Vienne et al., 1996). The development of apomictic seed has three stages: (i) suppression of meiosis (apomeiosis), (ii) endosperm formation without fertilization (parthenogenensis), and (iii) seed formation with fertilization (pseudo-apomixis) or without fertilization (autonomous apomixis) (Kandemir and Saygili, 2015). In pseudo-apomixis, the young embryo is aborted before mature embryo sac formation and replaced by developing aposporous sacs (Barcaccia and Albertini, 2013).

Apomixis has been explored in pearl millet largely for fixing hybrid vigor. The feasibility of interspecific transfer of genes for apomixis from *P. orientale* into pearl millet was investigated by Hanna and Dujardin (1982). The interspecific hybrids produced by pollinating CMS pearl millet (Tift 23DA) with *P. orientale* pollen had 2n = 25 with seven large *P. glaucum* and 18 small *P. orientale* chromosomes. The 18 *P. orientale* chromosomes paired mainly as bivalents, whereas the seven *P. glaucum* chromosomes remained univalents. This response demonstrated that the two species were not closely related. Three hybrids examined were found to be different: a highly apomictic (<5% sexual embryo sacs), an obligate apomict (the progeny is 100% maternal), and a facultative apomict (some progeny result from either a normal meiosis and/or a normal fertilization of the egg cell). Backcrossing the interspecific hybrids with pearl millet pollen produced ~25% of plants with 2n = 32 chromosomes (14 *P. glaucum* and 18 *P. orientale*), indicating the possibility of gene transfer between these two species. The interspecific hybrids were immune to rust and leaf spot, unlike the susceptible CMS female parent Tift 23DA.

The possibility of apomictic reproduction in non-polypl oid pearl millet was established by the formation of polyploid plants (2n = 21) in a uniformly open-pollinated progeny of an apomictic interspecific hybrid between *P. squamulatum* and *P. glaucum* (Dujardin and Hanna, 1986). Although the apomictic trait has not been introduced into major crops, it has been transferred from *P. squamulatum* (2n = 6x = 54) into tetraploid pearl millet through a trispecific hybrid crossing scheme (Dujardin and Hanna, 1989b, 1989c). This finding represented a breakthrough in transferring apomixis from wild species into cultivated species. It required a third bridging species, *P. purpureum* (2n = 4x = 28) and the development of an autotetraploid *P. glaucum* (2n = 4x = 28) to cross with the hexaploid *P. squamulatum* (Dujardin and Hanna, 1989c). The resulting trispecific hybrid was then backcrossed to tetraploid pearl millet to produce an obligate apomictic plant. However, the apomictic plant had low seed set under self- or open pollination (6.4%) (Dujardin and Hanna, 1989b). The low seed set was thought to be the result of poor pollen fertility that may have occurred from doubling the chromosome number of the diploid pearl millet (Dujardin and Hanna, 1989c), or from endosperm imbalance (Morgan et al., 1998). Intercrossing of the two semisterile tetraploid
inbred lines improved fertility. This finding was probably attributable to genetic incompatibility that was partially overcome with heterozygosity (Dujardin and Hanna, 1989c). The increased fertility resulted in enhanced pollen shed, seed set, seed quality, and seed germination.

The successful application of apomixis in plant breeding depends on the availability of cross-compatible sexual and apomictic plants. Molecular relationships between apomictic and sexual reproduction were unknown until the early 2000s (Bicknell and Koltunow, 2004). Therefore, comparative analyses of apomictic and sexual reproduction in appropriate model systems need to be conducted for the successful application of apomixis in plant breeding and seed production (Bicknell and Koltunow, 2004).

CULTIVAR RELEASE AND GERMPLASM REGISTRATION

The pearl millet breeding programs established at Georgia Coastal Plain Experiment Station in Tifton, the Agricultural Research Center–Hays, and the University of Nebraska–Lincoln have been involved in germplasm enhancement, parent inbred line development for hybrid cultivars, and breeding for stress tolerance. There have been several forage and grain hybrid cultivars released as commercial cultivars exclusively by the Georgia Coastal Plain Experiment Station, Tifton (Table 2). The forage hybrids released are leafy semidwarf types with high leaf-to-stem ratio. The two commercial grain hybrids released from the Georgia program were HGM 100 and TifGrain 102 (Hanna et al., 2005a, 2005b). HGM 100 was released in 1991 (Gulia et al., 2007). It was widely planted soon after its release, with successful harvest and good yields. TifGrain 102 was a hybrid (Tift 99D2 A1 × Tift 454). It represented a new generation of pearl millet hybrids for grain production. TifGrain 102 is characterized by shorter plant height, earlier maturity, larger grain size, and better combine harvest than earlier cultivars. In addition, it has resistance to root-knot nematodes and rust. This hybrid yields 4000 to 6000 kg ha\(^{-1}\) of grain without irrigation in the southern Coastal Plain and the Great Plains of the United States (Hanna and Wilson, 2002).

The three breeding programs also submitted a total of 42 accessions to GRIN (Supplemental Table S1). These accessions included enhanced germplasm, breeding lines, and inbred seed and pollinator parents developed by University of Nebraska–Lincoln (24 accessions), Georgia Coastal Plain Experiment Station–Tifton (16 accessions), and K-State (two accessions). Several semidwarf and early-maturing parental lines developed by the Agricultural Research Center–Hays of K-State are not formally registered yet. The newly initiated breeding program will use these previously developed parental lines, document their merit, and preserve them for future use in the breeding program.

For the pearl millet breeding success in India, ICRISAT partnership-based genetic improvement has been instrumental in development and dissemination of valuable germplasm since the 1970s. The early work of ICRISAT was focused on developing a diverse range of trait-specific composites, recurrent selection for grain yield and downy mildew resistance, and development of OPVs (Rai and Kumar, 1994). With a strategic shift in the early 1990s that aligned with regional players, ICRISAT developed and disseminated >180 hybrid parents and trait-based breeding lines (Rai et al., 2014). The widespread adoption of high-yielding and downy mildew–resistant hybrids brought about a quadruple increase in grain yield (24 kg ha\(^{-1}\) yr\(^{-1}\)) since the mid-1990s, compared with 6 kg ha\(^{-1}\) yr\(^{-1}\) obtained before the 1980s (Yadav and Rai, 2013). As a result, a total of 138 hybrids by the public sector and 52 hybrids by the private sector breeding programs have been released in India since the 1960s (Singh et al., 2014).

FUTURE RESEARCH IMPLICATIONS

Wide genetic variation relative to growth habit, light requirement, temperature response, grain and forage yield, and grain and forage nutritional quality has been reported in pearl millet. This genetic variation is promising for further improvement in pearl millet grain and forage yields. Hence, extensive collection and characterization of pearl millet germplasm as potential sources of genetic variation relative to target traits are essential for developing a successful pearl millet breeding program.

Given its superior tolerance to drought, high temperature, and salinity compared with many other cereals, pearl millet has potential to become an alternative food and feed crop in the United States. However, the weakening in pearl millet breeding efforts has negatively influenced

Table 2. Pearl millet forage and grain hybrid cultivars released in the United States.

<table>
<thead>
<tr>
<th>Name/code</th>
<th>Pedigree</th>
<th>Major characteristics</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gahi 3</td>
<td>Tift 23D(_A) (D_p) × Tift 186</td>
<td>Tall, leafspot resistant</td>
<td>Burton (1977)</td>
</tr>
<tr>
<td>TifLeaf 2</td>
<td>Tift 85D(_A) (D_p)/Tift 383</td>
<td>First dwarf leafy forage hybrid, rust resistant</td>
<td>Hanna et al. (1988)</td>
</tr>
<tr>
<td>TifLeaf 3</td>
<td>Three-way hybrid between Tift 85D(_A), Tift 8593, and Tift 383</td>
<td>Semidwarf, leafy, high-quality forage hybrid</td>
<td>Hanna et al. (1997)</td>
</tr>
<tr>
<td>Tift 8593</td>
<td>Tift 85D(A)/Tift 93</td>
<td>Used to produce TifLeaf 3, long panicle</td>
<td>Hanna (1997)</td>
</tr>
<tr>
<td>HGM(™) 100</td>
<td>–†</td>
<td>Released in 1991, became susceptibility to rust</td>
<td>–†</td>
</tr>
<tr>
<td>TifGrain 102</td>
<td>Tift 99D2 A1/Tift 454</td>
<td>Shorter, earlier maturing, slightly larger grain hybrid</td>
<td>Hanna et al. (2005a, 2005b)</td>
</tr>
</tbody>
</table>

† No information available.
its improvement in recent years in the United States. The breeding programs at Tifton and Lincoln were discontinued for lack of new breeders. Fortunately, the Kansas pearl millet breeding program has resumed after a 16-yr hiatus. To improve pearl millet as a vital food and feed cereal that is widely accepted by producers in the drought-prone areas, its yield potential needs to be improved. Future research on pearl millet should focus on improving grain yield and nutritional quality for the resource-poor farmers in Africa and Asia. It is also important to continue to develop specific phenotyping platforms for high temperature and drought tolerance and to improve biotic and abiotic stress tolerance by harnessing the genetic variability present in the germplasm.

Furthermore, pearl millet is a climate-resilient crop and has great potential as an excellent genomic resource for isolation of candidate genes for tolerance to drought and heat stresses. Understanding the mechanisms of its adaptation to suboptimal climatic and edaphic conditions is expected to accelerate further genetic improvement of the crop and warrant possible deployment in the genetic improvement of other related crops. Thus, modern breeding tools and platforms need to be explored to better target key traits and accelerate the cultivar development using marker-assisted selection and/or genomic selection. High-throughput genome assays via next-generation sequencing of many germplasm accessions will be needed to characterize natural genetic variation within the germplasm and to discover sequence-based molecular markers associated with important agronomic traits. This approach should enhance opportunities in pearl millet improvement, cultivar development for future use, and potential spillover to other crops. It is anticipated that the currently ongoing pearl millet genome sequencing will be completed and information released soon to enhance the genetic and genomic studies.

In addition to its adaptation to dry, hot, and low-soil-fertility conditions, pearl millet has nutritional value that is better than, or at least comparable with wheat, rice, maize, and sorghum. Harnessing the available genetic diversity is immediately needed for nutritional quality improvement. Resources should be provided to facilitate breeding by use of molecular technologies already available. Development of food products from pearl millet should also be an area of research to make pearl millet acceptable as an alternative crop of the future.

Conflict of Interest
The authors declare that there is no conflict of interest.

Supplemental Material Available
Supplemental material for this article is available online.


Stepmeyer, W.D. 1990. Pearl millet breeding. INTSORMIL Annu. Rep. Univ. of Nebraska, Lincoln, NE.


