Breeding for Yield and Adaptation

C. Aruna and R. Madhusudhana

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Abstract

Sorghum is the dietary staple for millions of people living in the subtropical and semi-arid regions of the globe. Its cultivation around the world is spread over diverse agro-ecosystems. In almost all the sorghum-growing regions, the grain yield levels have been enhanced over the years because of improved cultivars with higher nutrient response and better crop management practices. In every sorghum improvement program, yield and adaptation are the primary objectives for improvement. Wide genetic diversity is available in the cultivated *Sorghum bicolor*, as reflected in its five basic races, viz., *bicolor*, *kafir*, *guinea*, *caudatum*, and *durra*, and their ten intermediate races. The *Zera-zera* (an intermediate race between *caudatum* and *guinea*) landraces from Ethiopia and Sudan have proved to be useful sources for many traits such as excellent grain quality, high grain yield potential, tan plant, resistance to leaf diseases, and desirable plant type. Despite the considerable diversity in the available germplasm, very few germplasm lines have been utilized in the breeding for yield and adaptation so far. The

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diversity among the five basic races needs to be exploited to broaden the genetic base to produce cultivars with higher yield and adaptation for sustainable production.

Keywords

Genetic diversity · Races and intermediate races · Yield enhancement

1 Introduction

Sorghum, a staple food for over 500 million people in the semiarid tropics of Africa and Asia, is highly adapted to drought and high temperatures. It is playing an increasingly important role in meeting the challenges of feeding the world's growing population under the climate change scenario. Globally, sorghum is positioned as the fifth most economically important cereal after wheat, rice, maize, and pearl millet and plays a critical role in providing food, feed, fodder, and fuel and provides half of the world's food calories (Reynolds et al. 2016). Sorghum being an important C4 plant has higher photosynthetic ability and greater nitrogen and water use efficiency. It is suitable to hot and dry agro-ecologies which are subjected to frequent droughts and plays an important role in ensuring food security in this region. Sorghum research has not received the required attention among the scientific community especially in Africa and Asia in the past because it is considered as a coarse grain and much of its production is at subsistence level. However, increased food demand due to rapid population growth, enhanced utilization of animal products, and depleting fossil fuel reserves has necessitated for utilizing the full potential of this crop as food, feed, fodder, and fuel. For enhancing the productivity of a crop, genetic improvement is the most cost-effective means.

Genetic improvement of sorghum is being addressed by many national and international programs globally, viz., USDA (United States Department of Agriculture), INTSORMIL, the International Crops Research Institute for the Semi-Arid tropics (ICRISAT), FAO/UNDP (Food and Agricultural organization of the UN and the United Nations Development Program), ICAR-Indian Institute of Millets Research (ICAR-IIMR), and many other national research organizations in different countries such as Africa, Australia, and China. The objectives of these sorghum improvement programs differ in different countries and regions depending on the local production environment, constraints, and end-product utilization. At present sorghum cultivation is spread across diverse agro-ecosystems and its improvement has been characterized by long term increase of grain yields (Miller and Kebede 1984; Doggett 1988) and evolving more adaptive genotypes to cope with increasingly diverse environmental conditions under the climate change scenario. Since sorghums are tropical in origin, the important factors that define its adaptability are light, temperature, and day length (Kimber 2000). Diverse germplasm has been utilized in different breeding programs aiming at improved yield and adaptation.

2 Genetic Diversity Utilized in Breeding Programs

The diversity available in the cultivated species of *Sorghum bicolor* is reflected in its five basic races, viz., *bicolor*, *kafir*, *guinea*, *caudatum*, and *durra*, and their ten intermediate races. National and international research programs have used some of the germplasm to broaden the genetic base of the material for the traits of interest (House et al. 1996) and developed elite cultivars for food and feed purposes. Sorghum germplasm collections are unique in terms of size and diversity thus providing enormous genetic variability for the crop improvement programs (Dahlberg et al. 1996). The nuclear-cytoplasmic male sterility system which has formed the basis for exploiting hybrid vigor was contributed by *kafir* race in combination with *durra* from eastern Africa. While *caudatum* and *durra* races have contributed genes for higher yields, *guinea* from West Africa provided the genes for resistance to grain molds, and *bicolor* race contributed for forage sorghum breeding (Kameswara Rao et al. 2004). Indian *durras* have contributed genes for resistance to shoot fly and drought. Majority of the germplasm has been utilized for improvement of agronomical and adaptive traits, some target traits being increased seed number, larger panicle size, plant biomass, drought tolerance, disease resistance, greater leaf area indices, increased green leaf retention, and greater partitioning of dry matter that contributes to increased yields (Miller and Kebede 1984). Diverse sorghum germplasm is available in Africa, the primary center of its origin, and different parts of the world have different collection of the germplasm. Breeding programs across the world have utilized the diverse germplasm available in Ethiopian collections which consist of three distinct sorghum types, *Zera-zera*, a *caudatum* type of sorghum from lowland, humid areas; *durras*, which are found mostly in lower to mid-elevations; and high-altitude sorghums, which are made up of primarily *durra-bicolor* derivatives (Upadhyaya et al. 2014). Especially, the *Zera-zera* have been extremely useful for the improvement of food type sorghums, contributing both tan plant and high-quality seed (Rosenow and Dahlberg 2000).

Sudan also is a rich source of trait diversity, where *Caudatum* race dominates and *caudatum-durras* and *caudatum-nigricans* are observed in the higher rainfall areas of central Sudan and *Zera-zera* type in Eastern Sudan. While Southern Sudan has *caudatum* and *caudatum-guinea* derivatives, western Sudan has "*zinnari*" germplasm (*durra* derivatives). *Zinnari* germplasm is characterized with large panicles, large seed, and long, stiff rachis branches, and these were documented to have good acid soil tolerance. River valleys of northern Sudan were found to have some true *durras* which were useful as sources of drought resistance (Rosenow and Dahlberg 2000; Rosenow et al. 1999). True *guineas* are found in West Africa, especially in central and southern Mali, Burkina Faso, and a portion of Senegal. *Masakwa* sorghums of western Africa are suitable for transplanting. In China, *bicolor* or *bicolor* derivatives are the most indigenous land races, with many in the working group *nervosum*, commonly called *kaoliangs*. Chinese lines were found to be distinct and formed a different cluster from the other world collection (de Oliveira et al. 1996). Tolerance to low temperatures was observed in germplasm collected in

Ethiopia, Uganda, Yemen, and highlands of Kenya, Zaire, and Cameroon (Kimber 2000).

Initially in almost all the breeding programs, especially in Africa and India, varieties were developed through pure line selections within cultivated landraces. About 34 germplasm accessions were directly released as cultivars in 17 countries, with some of these released in more than one country (Upadhyaya et al. 2014). The classic example of sorghum germplasm utilization is the conversion program undertaken by Texas A&M-USDA (Dahlberg et al. 1996) which was initiated to convert tall, late maturing tropical sorghums to short and early types using backcrossing program (Rosenow and Dahlberg 2000). The lines developed from the sorghum conversion program have made large contribution to the sorghum improvement programs in the United States and elsewhere (Rooney 2004). It was observed that these converted lines are excellent sources of resistance to diseases, insects, drought, lodging, and grain weathering and possess plant and grain characteristics potentially useful in improving the food and feed value of grain sorghum (Duncan et al. 1991). Some converted Ethiopian germplasm are the *Zera-zera*, SC 108 (IS 12608C), and SC 110 (IS 12610C), SC 170 (IS 12661C), SC 173 (IS 12664C), the midge resistant line SC 175 (IS 12666C), durras with stay-green SC 35 (IS 12555C) and SC 33 (IS 12553C), and a *durra-bicolor* with downy mildew, head smut (*Sporisorium reilianum*) and anthracnose (*Colletotrichum graminicola*) resistance, SC 155 (IS 12645C). Also, SC 326-6, a IS 3756 derivative has resistance to rust, anthracnose, leaf blight (*Exserohilum turcicum*), and other leaf diseases (Rosenow and Dahlberg 2000). Other very useful converted exotics have been SC 56 (IS 12568C), a stay-green and lodging-resistant line, SC 414 (IS 2508C), a downy mildew resistant line with wide adaptation, SC 748 (IS 3552C), a grain mold and weathering-resistant line, and SC 120 (IS 2816C), a leaf disease-resistant line.

3 Cultivar Option

Since sorghum is an often-cross pollinated crop, the crop improvement methods applicable to both self- and cross-pollinated crops can be conveniently used for cultivar development. Hence one can find sorghum pure line varieties, F_1 hybrids, and populations as cultivar options in different parts of the world. Lot of information is available on available genetic variability in sorghum and heritability and inheritance pattern of important yield contributing traits. Initially only pure line selections were followed in the farmers' varieties and local land races. With the discovery of cytoplasmic-nuclear male sterility (Stephens and Holland 1954), sorghum hybrid development and exploitation has gone to commercial level. Most breeding programs focused on the development of F_1 hybrid parents. The restorer lines developed in this process become good candidates for development of open pollinated varieties (OPVs). While in most of the developed countries, hybrids are the preferred cultivars, sorghum producers in some areas in Africa, and post-rainy sorghum areas in India rely still on open pollinated cultivars. The main reasons why hybrids are not popular in these regions being either limited heterosis due to narrow genetic base or lack of well-established seed industry for hybrid production and marketing.

The cultivation of F_1 hybrids has been increasing, particularly in China, India, and South Africa. Hybrids have greater response compared to varieties, particularly land races and that has encouraged the use of fertilizer and improved management practices (House et al. 2000). A yield advantage of 20–60% with hybrids was recorded compared to improved varieties. Hybrids are more stable across environments and under stress; the yield decline in hybrids is comparatively less (House et al. 1996). The absence of a mechanism for hybrid seed production and distribution has been a major hurdle and a discouraging factor in several countries. In India and African countries, off season nurseries have been established to make hybrids which help in speeding up breeding progress. Maunder (1972) reported 150% increase in sorghum yield during the first 15 years of hybrid sorghum cultivation in the United States. Miller and Kebede (1984) reported an annual yield gain of 7% in the sorghum improvement program of the United States for the period of 1950–1980. Though many of the current hybrids are based on A_1 cytoplasm, sorghum hybrids on A_2 cytoplasm have been grown annually on about 200,000 ha since the early 1980s in China (Chen and Shi 1995).

These advances in sorghum hybrid development has significantly contributed to yield gains in countries like China, the United States, Australia, Brazil, Mexico, and India (Rakshit et al. 2014). Influence of sorghum hybrids in achieving yield gains in different countries is well documented (Smith and Frederiksen 2000 in United States; Stephens et al. 2012 in Australia; Gizzi and Gambin 2016 in Argentina; Aruna and Deepika 2018 in India). The quantum jumps in sorghum grain yields under rainfed conditions are attributed to a combination of genes for reduced plant height, better grain/straw ratio, and good responsiveness to added nutrients (House et al. 2000).

4 Breeding for Grain Yield and Adaptive Traits

Sorghum yield productivity is highly variable and is influenced by genotype, environment, and their interaction. There has been a huge yield gap in the realization of the crop potential against the documented highest yield potential of 15,000 kg ha^{-1} (Rooney 2004). This clearly indicates the opportunities available to enhance the yield potential of the sorghum crop not only by genetic manipulations but also by reducing the environmental constraints.

Yield and adaptation are the central objectives of any crop improvement program. A more adaptive genotype maintains high production in different environments even in the presence of stress. All sorghum cultivars in general have the genetic/physiological potential to produce some degree of economic yield; it varies with the adaptive traits a genotype has which helps in coping up with the environment (yield = genotype × environment). A high yielding, widely adapted cultivar is one that responds positively to varying environmental changes (Miller et al. 1996).

To develop genotypes with wider adaptation, it is important to understand the genetics and relations between yield, maturity, and height (Rooney 2004). In general, grain yield is strongly correlated with increased maturity. But in case of stress, like drought encountered during the growing season, the positive relationship between grain yield and maturity is eliminated, and in most cases earlier maturity cultivars out yield late cultivars. Hence early maturity cultivars are the preferred genotypes in dryland environments where drought stress and/or short growing seasons are consistently encountered.

Like any other crop, grain yield in sorghum is a complex trait controlled by many genes (Beil and Atkins 1967; Aruna and Audilakshmi 2008). Grain yield is determined by grain number, grain size, panicle length, and number of primary and secondary branches. Genes controlling these component traits act either additively or epistatically to define the final output of grain yield. All these component traits are quantitative and are influenced by environment. Genetic improvement of grain yield is a challenging task as it involves accumulation of positive alleles involved in the expression of component traits. Over the last decade, few studies in sorghum have identified QTL for grain yield and its component traits (Brown et al. 2006; Hart et al. 2001; Nagaraja Reddy et al. 2013; Ritter et al. 2008; Srinivas et al. 2009; Sukumaran et al. 2016; Bernardino et al. 2019). The major component traits for yield are number of kernels per panicle, size of kernels, and number of panicles per unit area (Miller et al. 1996). The kernel size and number are shown to be strongly negatively correlated. However, that negative correlation can be broken by selecting females of hybrids with high number of kernels, then selecting male parents (R lines) with large kernels. Non-overlapping loci for grain number and weight were identified suggesting that these traits can be manipulated independently to increase the grain yield in sorghum (Boyles et al. 2016). These independent loci for grain number and thousand grain weight can be incorporated into elite cultivars thus potentially increasing one yield component without decreasing the other, ultimately increasing total grain yield. The genetic basis of grain weight has been studied in multiple linkage analysis studies in sorghum (Brown et al. 2006; Feltus et al. 2006; Murray et al. 2008; Paterson et al. 1995; Pereira et al. 1995; Rami et al. 1998; Srinivas et al. 2009; Tao et al. 2018; Tuinstra et al. 1997) which together identified 12 unique genomic regions (Mace and Jordan 2011). More recently, sorghum diversity panels have been used to identify loci significantly associated with grain weight and other grain yield component traits (Boyles et al. 2016; Zhang et al. 2015).

Plant height and grain yield usually have a positive relationship under favorable environment. Plant height in sorghum is a complex trait consisting of number and length of internodes and the peduncle length. Four major effect genes (Dw1, Dw2, Dw3, and Dw4) have been described in sorghum with significant effect on plant height with a modifier complex of eight genes that influenced elongation of internodes (Karper and Quinby 1954). The four genes are inherited independently. Tall is partially dominant to dwarf and the effect of the loci is cumulative (Karper and Quinby 1954) but unequal. The dwarfing effect of recessive genes (dwdw) at any of the four loci is brachytic (where internode length is reduced, but not peduncle length). The genotype with all four dominant alleles (zero dwarf) may reach a height of up to 4 m. Recessive allele substitution may reduce height by 50 cm or more. If one or more height loci are in recessive condition, recessivity at additional loci may not have greater reducing effect on plant height. The 3-gene dwarf and 4-gene dwarfs may differ in height for 10–15 cm. Of the four major loci, Dw3 is highly unstable, and it mutates at a higher frequency of 1 in 600 plants (Karper 1932) leading to appearance of taller plants in dwarf genotypes. Dw1 and Dw2 are highly stable, whereas Dw4 has shown little instability in its action. Height loci show complementary effects, and hence they can be exploited to develop tall hybrids using two shorter genotypes. Despite growing conditions that affect plant height in varied environments, the general response of height is relatively consistent. Cassady (1965) and Graham and Lessman (1966) studied the allelic effect of Dw3 vs dw3 and Dw2 vs. dw2 on grain yield involving isogenic lines. In both studies, the dominant allele improved grain yields. It was suggested that better spatial arrangement of the leaves on Dw2 and Dw3 plants could have resulted in more efficient utilization of light.

Another adaptive trait which determines the extent of distribution of a crop in diverse climatic conditions is the flowering time (Bhosale et al. 2012; Craufurd et al. 1999). Though grain sorghum is a short-day plant and mostly photoperiod sensitive, there are genotypes which exhibit differential sensitivity to varying photoperiods and temperature regimes (Doggett 1988). Sorghum had a photoperiod controlled reproductive system to cope with the monsoon rainfall pattern, which followed the annual high-sun position. For maturity, four major genes (Ma_1, Ma_2, Ma_3 and Ma_4) with qualitative effect have been described, with multiple alleles at each locus (Quinby 1967, 1974). Tropical sorghums are usually dominant (*Ma*-) at all four loci and recessive condition (*mama*) at any one of the four loci leads to more adaptation to temperate climatic conditions. Maturity genes do interact and Ma_1 has maximum effect on the maturity and it influences the operation of other three genes (Ma_2, Ma_3 and Ma_4). Mutations in Ma_1 were critical for the early domestication and dispersal of sorghum from its center of origin across Africa and Asia (Quinby 1967). Dominance at Ma_1 locus (Ma_1-), Ma_2, Ma_3, and Ma_4 cause lateness, but when Ma_1 is recessive (ma_1ma_1), then even recessivity at other three loci (ma_2ma_2, ma_3ma_3 and ma_4ma_4) show dominance. The presence of the ma_3^R allele causes extreme earliness regardless of the genotypes present at any other locus. Most of the converted lines from tropical to temperate are recessive at first maturity locus (ma_1ma_1) and dominant at other loci. Tropical lines of early or late maturity retained their flowering behavior after their conversion to temperate zone adaptation. This was thought to be due to different alleles at one or more of the maturity loci, and not due to a group of modifying genes at other loci (Quinby 1967). Rooney and Aydin (1999) identified two dominant loci, Ma_5 and Ma_6, controlling photoperiod-sensitive response. Both Ma_1 and Ma_3 have been cloned. Ma_3 encodes a phytochrome B (Childs et al. 1997). The gene encoding pseudo-response regulator protein 37 (*PRR37*) was identified as a likely gene candidate for Ma_1 based on the known roles of PRR genes in flowering of *Arabidopsis* (Murphy et al. 2011). Ma_1 suppresses flowering by activating the floral inhibitor CONSTANS and repressing the floral activators, Early Heading Date 1, and FLOWERING LOCUS T. Mutations in Ma_1 produced early-maturing grain sorghum plants. Sorghum *Ma*$_6$, a strong repressor of flowering in long days, was identified as the CONSTANS, CO-like, and TOC1 (CCT)-domain protein encoded by *SbGhd7* (Murphy et al. 2014). Sorghum *Ghd7* increases photoperiod sensitivity and delays flowering by inhibiting expression of the floral activator SbEhd1 and genes encoding FT. Sorghum germplasm, both photoperiod sensitive and photoperiod insensitive, remain important sources of new genes for the continued development of cultivars and hybrids in terms of improvement in yield and resistance to biotic and abiotic stresses.

5 Breeding for Photoperiod-Sensitive Sorghums

In tropical regions, farmers' selection was for sorghum with specific daylength requirements that match local environmental conditions so that some grain production is assured. Small farmers are benefitted tremendously because no change in day length requirements is needed and hence there is no need to alter their cropping systems (Gomez and Chanterau 1996). Photoperiod-sensitive cultivars are in use in some areas, particularly in West Africa and the post-rainy sorghums of India. The informal selection by farmers for daylength sensitivity has resulted in sorghum that matures as available soil water is exhausted in the early part of the dry season, thereby ensuring that the crop fully utilizes the growing season. This is particularly beneficial if sowing must be done several times, but the crop should mature when there is still adequate moisture to finish grain formation (House et al. 2000). In Nigeria, photosensitive sorghum cultivars are available in which the date of planting controls the vegetative development of the genotype, but the duration and time of flowering and fruiting phases remain stable (Franquin 1984).

An example for photoperiod-sensitive sorghum is the unique group of sorghum called maicillos in Central America. These were introduced from Africa and were adapted to local farming practices. High photoperiod sensitivity of maicillos enabled them to become intercropped with early maize landraces (Gomez and Chanterau 1996). Crop improvement work on these lines by Meckenstock (1991) showed that these are extremely sensitive to photoperiod due to the presence of dominant alleles at the Ma$_1$ and probably the Ma$_2$ loci. Crosses were made between selected maicillos and elite germplasm in the early 1980s to develop a new enhanced photosensitive germplasm, combining excellent adaptation, better yield potential, and superior grain quality. These improved maicillos are of short stature with longer panicles and resistance to important diseases such as anthracnose, rust, gray leaf spot, downy mildew, and tan plant color, in addition to maintaining the photoperiodic response (Gomez 1995). Scientists working with the tropical germplasm in the United States and India have studied many aspects of the photoperiod response and understood the genetics, physiology, and breeding methodologies of photoperiod-sensitive sorghum (Gomez and Chanterau 1996), enabling tropical plant breeders to tailor sorghum genotypes based on photoperiod requirements.

6 Breeding for Photoperiod-Insensitive Sorghums

Photoperiod insensitivity in sorghum allows the breeding and development of cultivars to suit different environments. These lines can be directly utilized in making crosses at any location. Most breeding programs around the world have worked primarily with photoperiod-insensitive or relative non-sensitive types. A few examples of widely used photoperiod-insensitive exotic sorghums include Sureno, a grain mold-resistant line; SRN39, a striga-resistant line; Malisor 84-7, a headbug-resistant line; and CS3541, Macia for high yield and adaptation (Rosenow and Dahlberg 2000). Generally, the removal of maturity gene, Ma_1, will remove the response to photoperiod. The interaction of Ma_5 and Ma_6 is also a photoperiod phenomenon but is not of significance in most germplasm. When these two genetic conditions are addressed, response to varying photoperiod is minimal, and the remaining variations in growth and development are primarily temperature driven. If the confounding effect created by photoperiod sensitivity is removed, yield and its stability could be enhanced through selection for yield components. Manipulation of maturity as an adaptive trait has provided for higher and more stable yields in many areas of the world, i.e., early maturing sorghums in drought prone or short duration seasons vs. late maturing sorghums in well-watered, longer duration seasons. Growers tend to use hybrids that mature as late as environmental conditions permit to maximize yields. However, once photoperiod insensitivity is established, responses to biotic and abiotic stresses are exposed, for which solutions are to be devised. Some detrimental effects of photoperiod among photoperiod-insensitive types in tropical environments are the loss of leaf areas, elongated internodes, and rapid change from vegetative to reproductive growth. The use of adaptive trait breeding has been successful in achieving stable and productive genotypes. Identification and utilization of such traits as non-senescence and resistance to important pests and diseases have led to further improvement in yield and yield stability in many sorghum production areas. Removing the impact of photoperiod response will help in focusing the research in areas of physiological growth and development. Photoperiod insensitivity has allowed for continuous improvement of yield and adaptation in sorghum (Miller et al. 1996).

7 Future Needs

Demand for sorghum grain will continue to rise because of its suitability for diverse end uses both for food and non-food industries (Boyles et al. 2016). For sorghum to be more competitive, there is a need to improve the rate of yield gains which necessitates screening of world germplasm for yield genes. Though considerable diversity is available in the germplasm, very few lines have been utilized so far. There is a need to use the diversity among the five basic races to broaden the genetic base for producing improved cultivars. The *caudatum* race has been exploited well in breeding programs. Studies have shown that the guinea race contributes significantly (after *caudatum*) to higher mean and heterosis for grain yield (Aruna and

Audilakshmi 2008; Reddy et al. 2010). To utilize the available genetic diversity, it is important to identify major agronomic traits for each race/inter-race and incorporating them in elite background. Research collaborations across crops and across disciplines may accelerate genetic, physiological, and molecular understanding of important traits, which would increase the opportunities to enhance genetic yield potential of sorghum cultivars with under wider adaptation.

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