Chapter 12
Genomic-Assisted Enhancement in Stress Tolerance for Productivity Improvement in Sorghum

Kirandeep K. Romana, Girish Chander, Santosh Deshpande, and Rajeev Gupta

Abstract Sorghum [*Sorghum bicolor* (L.) Moench], the fifth most important cereal crop in the world after wheat, rice, maize, and barley, is a multipurpose crop widely grown for food, feed, fodder, forage, and fuel, vital to the food security of many of the world's poorest people living in fragile agroecological zones. Globally, sorghum is grown on ~42 million hectares area in ~100 countries of Africa, Asia, Oceania, and the Americas. Sorghum grain is used mostly as food (~55%), in the form of flat breads and porridges in Asia and Africa, and as feed (~33%) in the Americas. Stover of sorghum is an increasingly important source of dry season fodder for livestock, especially in South Asia. In India, area under sorghum cultivation has been drastically come down to less than one third in the last six decades but with a limited reduction in total production suggesting the high-yield potential of this crop. Sorghum productivity is far lower compared to its genetic potential owing to a limited exploitation of genetic and genomic resources developed in the recent past. Sorghum production is challenged by various abiotic and biotic stresses leading to a significant reduction in yield. Advances in modern genetics and genomics resources and tools could potentially help to further strengthen sorghum production by accelerating the rate of genetic gains and expediting the breeding cycle to develop cultivars with enhanced yield stability under stress. This chapter reviews the advances made in generating the genetic and genomics resources in sorghum and their interventions in improving the yield stability under abiotic and biotic stresses to improve the productivity of this climate-smart cereal.

Keywords Genomics · Markers · Molecular breeding · Nutrition · Sorghum · Stress tolerance

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12.1 Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is one of the most important robust and reliable cereal crops globally to feed around 500 million people who rely on it as a dietary staple (Dicko et al. 2006; ICRISAT 2018). It is the most common staple food in many semi-arid and tropical regions of the world because of its better adaptability and productivity under environmental stresses like droughts and high temperatures as compared with other cereals, namely, wheat, rice, and maize (Nedumaran et al. 2013; Reddy et al. 2012). Sorghum is often a multipurpose crop with dual benefits from stover as well as grain. Grain is used mainly as food or feed, whereas stover is a vital source of fodder for livestock. More than 35% of sorghum produced all over the world is used for human consumption and the rest as animal feed and production of alcohol and industrial products (Awika and Rooney 2004; Dicko et al. 2006). In sub-Saharan Africa (SSA) and South Asia (SA), sorghum grain is used as both human food and animal feed (including as poultry feed), whereas in the USA, Australia, Brazil, and other developed nations, it is used fundamentally as animal feed. With focus to address micronutrient malnutrition in about 2 billion people globally, promotion of crops, varieties, and agricultural practices that promote easy access of nutrient-dense food to rural masses is the most effective strategy (Wani and Chander 2016). In this context, sorghum along with pearl millet outshines as a choice crop having high contents of macro/micro-nutrient contents and meeting the nutritional requirements of people in SSA and SA. Improving the productivity and access through production in large areas, this crop could be an effective means to address undernourished children and women worldwide. Besides having important human health and nutritional qualities, sorghum is also a gluten-free cereal which makes it an alternate source of specialty foods for people with celiac disease who are allergic to gluten (Dicko et al. 2005; Rooney 2007).

Globally, sorghum is grown in about 42 million hectares area with a total production of 63 million tons from the year 2010 to 2016, across 98 countries in Africa, Asia, Oceania, and the Americas. Nigeria, India, the USA, Mexico, Sudan, China, and Argentina are the major sorghum-growing countries (Fig. 12.1). Other sorghum-producing countries include Burkina Faso, Chad, Ethiopia, Gambia, Ghana, Mali, Mauritania, Mozambique, Niger, Senegal, Somalia, Tanzania, and Yemen (FAOSTAT 2016). In countries like India, the productivity of sorghum in the year 2013 was reported to be quite low at about 850 kg per ha (FAO 2013) which suggest a huge potential to explore untapped genetic diversity in combination with modern genetics and genomics tools.

In India, the major sorghum-growing states are Karnataka, Maharashtra, Telangana, Andhra Pradesh, Madhya Pradesh, Tamil Nadu, Gujarat, and Rajasthan. In India, though, there is a decline in the sorghum cultivation area among all states, a significant increase in the productivity has been recorded. However, with increasing realization of global warming inducing climate change and increased health consciousness, focus on “climate-change ready” and nutritious crops like sorghum is regaining. As a consequence, in the USDA report (2016), an increase in the area

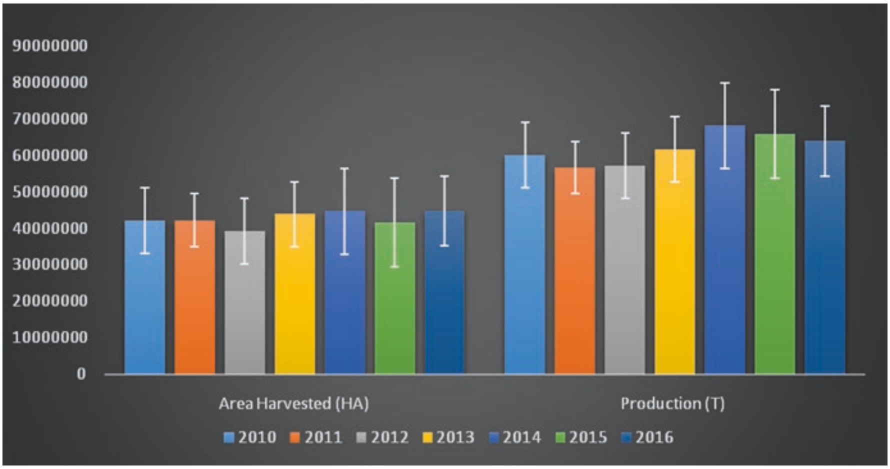

Fig. 12.1 Global sorghum productivity from the year 2010 to 2016. (Source: FAOSAT 2016)

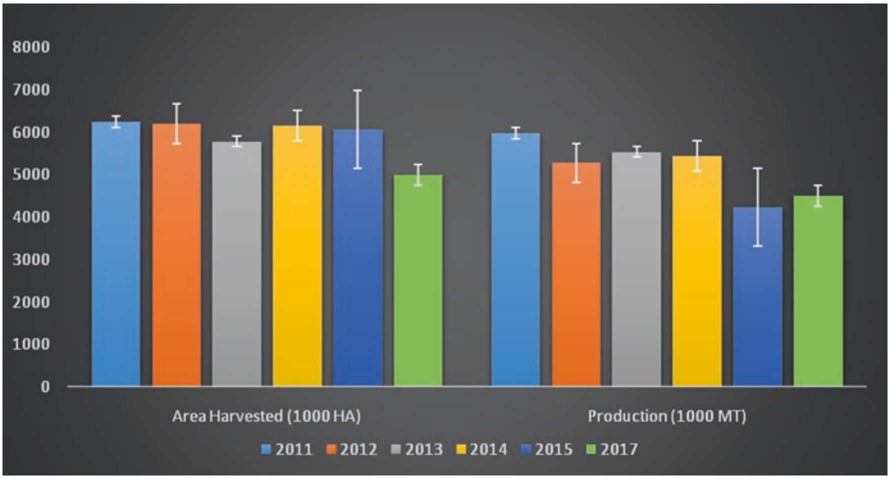

Fig. 12.2 Sorghum productivity in India from the year 2011 to 2017. (Source: USDA 2017)

of sorghum production by 19% and increase in grain harvest by 23% were observed globally (USDA 2016).

Sorghum production worldwide for the last 30 years revealed a declining trend in area under cultivation from 44.5 to 41.9 million hectares with corresponding decrease in production from 62.8 to 59.3 million metric tons (FAO Stat 2016). In India sorghum was grown in about 6245 (‘000 ha) in the year 2011 which has been reduced to 5000 (‘000 ha) during the year 2017 (Fig. 12.2). Similarly, sorghum production in India also showed decreasing trends from 5979 (1000 Mt) in the year 2011 to 4500 (1000 Mt) in the year 2017(USDA report 2017) (Fig. 12.2). In the present scenario of increasing effects of climate change on various crops and regions, sorghum stands a great chance to adapt to several abiotic and biotic stresses and ensure future food and nutritional security globally as well in regions with perennial chronic malnourishment and undernourishment.

Genetic studies and conventional plant breeding research coupled with other crop improvement interventions were able to address many of the biotic and abiotic stresses over the last half of the century. The current climatic change scenarios have exposed the sorghum crop to variations in diurnal temperature regimes and variations in rainfall patterns that have not been experienced before. The sorghum breeding research is trying to cope with these new challenges; the advances in new biological technologies including especially genomics have the potential to make these adjustments at a faster pace, with improved efficiency and in most cases at relatively lower investments. Here we reviewed the recent updates from genomics research for addressing stress tolerance improvement.

12.2 Genetic and Genomic Resources in Sorghum

Large numbers of genetic, genomic, translational, and mutational resources had become available in the recent years for sorghum, which further raises the research opportunities for sequence variations in relation to the phenotypic traits of interest and their further productive utilization in the sorghum improvement programs. The recent applications of the molecular markers and genomic technologies have shown promising effects in efficient breeding. However, the success of sustained gains in any crop relies on the variation of crop gene pool. The ICRISAT genebank maintains 41,023 sorghum accessions assembled from 93 countries which include land races, breeding material, advanced cultivars, and wild relatives (Upadhyaya et al. 2018). The core (~10% of total collection) and mini-core (~1% of total collection) representative and reference sets have been developed at ICRISAT for future research endeavors. These sets were further used to identify new sources of variations for stress resistance, phenology, seed yield, quality traits, etc. Great opportunities for the genetic improvement of sorghum are made available via reference genome sequence (Paterson et al. 2009), and diverse sorghum lines were further compared with a reference genome that leads to substantial untouched diversity. Access to large number of markers including genomic and EST-SSRs, DArTs (Mace et al. 2009; Ramu et al. 2010), and alignment of major trait genes and quantitative trait loci (QTL) to integrated linkage and physical map (Mace and Jordan, 2011) had fast-tracked integration of molecular marker technologies to dissect complex traits such as stress tolerances. With rapid advancements in next-generation sequencing (NGS) technologies, identification of large number of markers, especially single nucleotide polymorphism (SNP), has become cheap as compared to the other marker systems, especially wet lab-based assays. These NGS assays (such as genotyping-by-sequencing, GBS) identified large number of SNPs across genome and provide opportunities to identify SNPs present closest to or inside the genes associated with target traits. These identified SNPs can be converted to customized SNP assays using several platforms such as CAPS, KASP™ platform, or their modifications. Most of these platforms running SNP assays are inexpensive for fast-track and efficient utilization in breeding program either to transfer this trait or track the trait in target breeding populations. This will greatly improve the efficiency of introgression of component traits underlying different *stress tolerance* mechanisms by reducing breeding cycles (for recurrent parent recovery) and further recombining these for development of improved *stress*-tolerant cultivars. The recent examples of NGS application included genetic diversity and phylogenetic studies and trait mapping using genome-wide association mapping studies (GWAS). Morris et al. (2013) led to the discovery of approximately 265,000 single nucleotide polymorphisms (SNPs) in 971 worldwide accessions across Africa and Asia (which included the mini-core set, reference set and US sorghum association mapping panel) (Fig. 12.3). These findings were further reformed to diverse agroclimatic conditions. This phylogenetic study revealed that accessions cluster preferentially according to their geographic origin, followed by clustering into races or morphotypes. Utilizing the NGS technologies (Mace et al. 2013), resequenced 44 sorghum genotypes in which over 4.9 million SNPs were identified in *sorghum bicolor*. By utilizing gene-based population summary statistics of a prior selected candidate genes, 725 candidates were identified for domestication or improvement in sorghum (Mace et al. 2013). Recent initiatives of resequencing several hundred sorghum accessions such as TERRA-REF project (http://terraref.org/#genomic-and-genetic-data-and-computational-platform) targeting resequencing 1000 sorghum accessions for characterization of genetic variation and identification of genomic regions controlling biomass, plant architecture, and photosynthetic traits, and TERRA-MEPP project (https://terra-mepp.illinois.edu/team/ profile/michael-gore) will develop quantitative trait loci (QTL) models to predict daily plant biomass yield throughout the growing seasons.

Application of NGS tools like GbS for dissecting complex traits such as stress tolerance on DNA sequence level will capture most of the functional factors of genome related to trait expression. But other applications of NGS tools in RNA sequencing (commonly referred as RNA-seq) will help to capture the regulatory parts (Ozsolak and Milos 2011). For a complex trait such as stress tolerance/resistance, involving host-pest and/or environment interactions, many growth and development pathways are involved for its expression. Application of RNA-seq platforms can help understand the role of regulatory and transcription factors (including small RNA, microRNA) and their interaction with other pathways. There is big interest to utilize recent advances in RNA-seq technologies with the recombinants identified from fine-mapping exercise to move towards better understanding the stress tolerance in sorghum. Knowledge of QTL underlying stress tolerance traits can aid detection of resistance/tolerance genes (complex ➔ QTL) in sorghum.

Several genetic resources including, (i) germplasm panels such as mini-core set (Upadhyaya and Gowda 2009), sorghum reference set (Billot et al. 2013), and US sorghum association mapping panel (SAP); (ii) mapping populations such as random inbred line populations (over 10 RIL populations at ICRISAT-HQ, Patancheru; *Personal communication with Santosh Deshpande*) for several traits (Mace et al. 2013); (iii) nested association mapping (NAM) (Bouchet et al. 2017); (iv) backcross-based NAM (BCNAM) population, which can serve as genetic and breeding

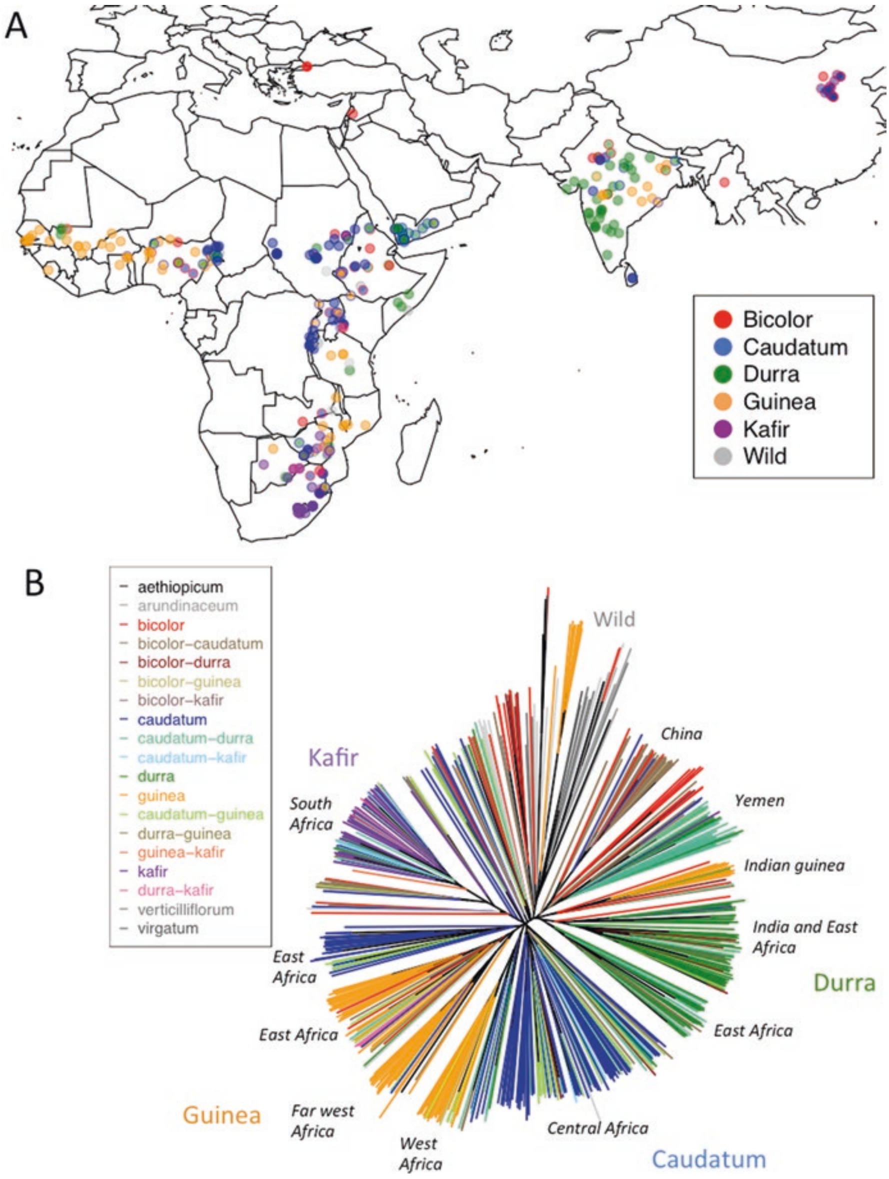

Fig. 12.3 Geographical and racial distribution of genetic diversity of sorghum accessions. (**a**) Geographic origin of 469 genetically diverse sorghum accessions studied by Morris et al. (2013); (**b**) neighbor-joining graph of the same 469 lines clustered into morphotypes within a region. (Source: Morris et al. (2013))

populations (Jordan et al. 2012); and (v) mutation populations such as TILLING population (Skelton 2014), are now available in sorghum. All these new tools play a major role in enhancing the breeding efficiencies by not only exploring genetic mechanisms but also providing or inducing new diversity in relatively elite backgrounds. These next-generation genetic resources are excellent tools for studying the connection between phenotype to genotypic variations. The BCNAM populations are already well established (Jordan et al. 2011) to benefit both trait mapping and introducing diversity that was not available previously in the traditional plant breeding populations. In sorghum improvement program at ICRISAT, BCNAM approach, in combination with other genomics tools, is currently being used extensively (Deshpande, unpublished) to address the priority traits related to yield, biotic and abiotic stress tolerance, etc. In terms of applications of these tools in molecular breeding, the NGS-based genotyping platforms such as whole genome resequencing (WGRS), genotyping-by-sequencing (GbS), etc., have the potential for molecular breeding (MB) and genomic selection (GS) which are emerging prediction tools in modern breeding programs. Considering the different levels of advancement of constituent technologies involved in GS, an appropriate resource investment strategy for every single breeding program needs to be developed for maximizing the rate of genetic gains. These resources provide the test bed for all genomics studies and their application for translational research for trait introgression and breeding applications.

12.3 Genomic Interventions for Abiotic Stress Tolerance

The conditions prevailed by abiotic stresses lead to extensive yield losses to agricultural production worldwide. Many researchers are instigating intensive research on various abiotic stresses such as drought, heat stress, and salinity (Bray et al. 2000; Cushman and Bohnert 2000). However, due to abiotic stresses, there is loss in the productivity of the crop to several degrees, and the losses were dependent on the time of onset, longevity, and stress intensity. Although sorghum is a harsh crop yet, drought is an important abiotic stress for sorghum. Other most important abiotic stresses in present era during cultivation are nutrient deficiency, aluminum stress, water logging, or temperature stress. The plants have to cope with all of them during cultivation along with high salinity and drought (Tari et al. 2012). The following section discusses some of major abiotic stresses in sorghum production.

12.3.1 Drought

Sorghum, one of the most drought-tolerant crops, is a dual-purpose crop. A detailed status on genomic interventions in abiotic stress tolerance in sorghum has been reviewed by Wang et al. (2014a, b). Water stress is the most important factor under climate change affecting the crop productivity (Araus et al. 2002). In the past, many positive efforts were made for improving tolerance of sorghum to drought through genetic enhancement (Mutava et al. 2011). Two different types of stress responses were observed in sorghum at distinct time interval, i.e., pre-flowering and post-flowering drought response (Harris et al. 2007). In sorghum, the green leaf area retention during the grain-filling stage has been found to be linked with sorghum post-flowering drought tolerance (Rakshit et al. 2016). As reported by Deshpande et al. (2016), seven sources for stay-green trait in sorghum have been used for QTL identification, such as B35 (Tuinstra et al. 1997; Crasta et al. 1999; Subudhi et al. 2000; Xu 2000a, b; Sanchez et al. 2002; Harris et al. 2007), E36–1 (Haussmann et al. 2002), QL41 (Tao et al. 2000), SC56 (Kebede et al. 2001), 296B (Srinivas et al. 2009), SC283 (Sabadin et al. 2012), and SDS 1948–3 (Habyarimana et al. 2010). A consensus map for the sorghum chromosome SBI-01 to SBI-05 (Fig. 12.4a) and SBI-06 to SBI-10 (Fig. 12.4b) exhibits the QTL intervals for stay-green QTLs from Mace and Jordan (2011) which were further aligned to

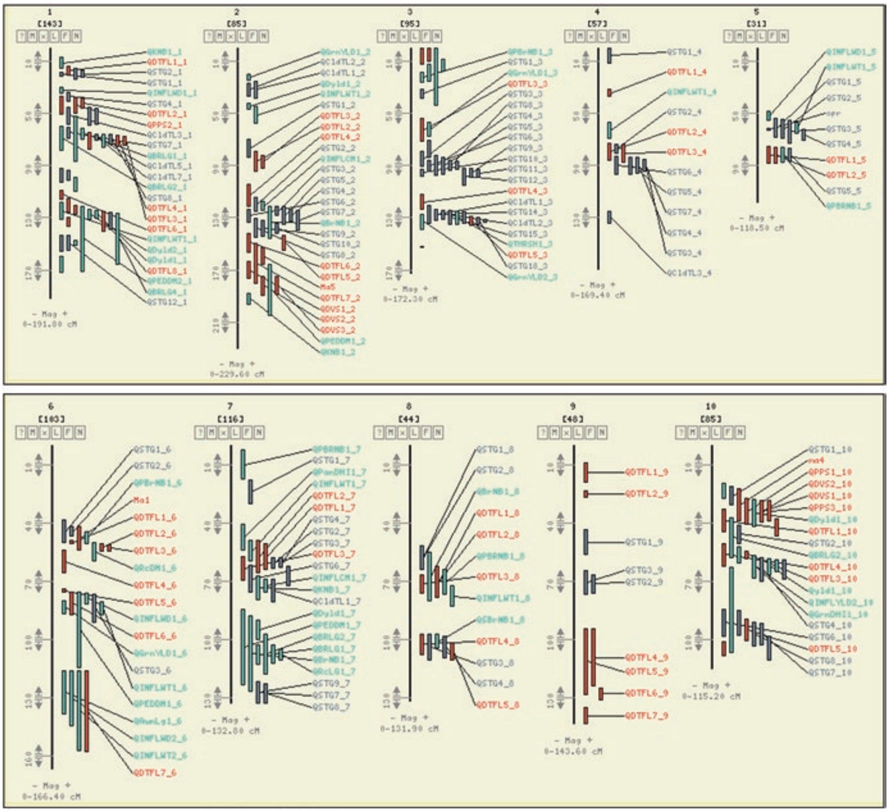

Fig. 12.4 (**a**) QTL tracks for sorghum chromosome SBI-01 to SBI-05. (**b**) QTL tracks for sorghum chromosome SBI-06 to SBI-10

physically aligned SSRs; the vertical bars in the map indicate the QTL interval tracks. The red color tracks in the map show up for the maturity genes/QTLs, and the aqua color is associated with panicle traits and gray color tracks for the stay green.

Stay-green QTL introgression research by Deshpande et al. (2016) was initiated at ICRISAT-HQ, Patancheru, India. This study led to the dissection of the genetic function of the stay-green QTLs, which suggested that *stg3A* and *stg3B* QTLs are responsible for transpiration efficiency and vapor pressure deficit response. In total, six QTLs were investigated, of which *stg3A* and *stg3B* QTLs were found to be more stable across genetic backgrounds and environments. The *stg3A* and *stg3B* QTLs are located next to each other on SBI-02, and the mesocarp gene, *Z*, which governs the grain seed coat color, is located in-between the two QTL intervals (Mace and Jordan (2010). For identification of the SNPs representing this targeted region in the sorghum genome, additional efforts are being made at ICRISAT (Deshpande et al. 2016).

For investigating the effects of stay-green introgression on stover fodder traits and grain-stover relationships, introgression of stay-green QTLs into sorghum S-35 and R-16 genetic backgrounds was executed at ICRISAT-HQ. Recently Blummel et al. (2015) have reported that one stay-green QTL (StgB) in S-35 increased the stover in vitro *organic matter digestibility* (IVOMD) along with grain and stover yield. Thus, a conclusion was drawn from the research that stay-green QTL can contribute to improve stover quality as well as grain and stover yield (Blummel et al. 2015).

For improving tolerance of post-flowering moisture stress in grain sorghum, a number of QTLs associated with stay green have been identified in sorghum for facilitation of its transfer for further adaptation. In the past few years, much research has been done for QTL discovery and consistency for stay-green traits, among these six major QTLs reported for stay-green traits, i.e., *stgC* (SBI-01), *stg3A* and *stg3B* (on SBI-02), *stg1* and *stg2* (on SBI-03), and *stg4* (on SBI-05) (Subudhi et al. 2000; Borrell et al. 2014). Detection, development, and influence of QTLs responsible for sorghum yield under drought tolerance were accomplished by many researchers (Tuinstra et al. 1998; Kebede et al. 2001). A very recent 2017 research, conducted by Jabereldar et al. (2017), on drought focuses on deficit irrigation scheduling practices on seed yield and water use efficiency of five sorghum genotypes. The results in this study highlighted that water stress at eighth leaf stage reduced the following traits, and reduction of length, panicle weight, number of grains per panicle, 100-grain weight, seed yield, and water use efficiency were also observed. There are many existing reports stating the presence of QTLs related to grain yield in sorghum for drought and cold tolerance or yield components (Sabadin et al. 2012; Phuong et al. 2013; Reddy et al. 2014; Kapanigowda et al. 2014). Also physiological parameters such as leaf greenness (chlorophyll content and chlorophyll fluorescence) play a pivotal role in its positive correlation to the grain yield under different conditions in sorghum (Xu 2000a; Harris et al. 2007).

12.3.2 Nitrogen Use Efficiency (NUE)

Nitrogen demand in agriculture is increasing across the world and is expected to reach up to approximately 250 million tons by the year 2050 (www.fao.org). It is well documented that almost 50% of the total nitrate applied is lost in the process of leaching, runoff and denitrification. This nitrate loss ultimately puts pressure on the cost of the crop production and lead to the pollution of water, soil and also contributes to greenhouse gas emissions. Therefore, development of genotypes or the crops with improved N absorption and utilization can lessen the problems of modern agriculture. With reference to nitrogen use efficiency (NUE), significant differences had been reported in sorghum genotypes (Maranville et al. 1980; Youngquist et al. 1992). Four N-tolerant sorghums, i.e., San Chi San, China17, KS78, and high-NUE bulk, and three sensitive genotypes such as CK60, BTx623, and low-NUE were used for bulk expression analysis studies under low N and normal N levels which revealed increased response of sensitive genotypes toward DEG transcripts associated with stress. However, tolerant genotypes showed increased root mass for efficient uptake of nutrients (Gelli et al. 2014). A population of 131 RILs derived from across between CK60 (inefficient N user) and China17 (efficient N user) were genotyped using GbS (Gelli et al. 2016), and multiple traits were found to be governed by the co-localized regions on chromosomal segments: SB-01, SB-05, SB-06, SB-07, and SB-09. The genomic regions of cloned QTLs and potential pleiotropic regions were equivalent for the genes associated with flowering time, *Ma3* on chromosome 1, and *Ma1* on chromosome 6, gene associated with plant height, *Dw2*, on chromosome 6. Further on the basis of the RNA sequencing data which represents the differential expression of transcripts related to nitrogen metabolism, glycolysis, seed storage proteins, plant hormone metabolism, and membrane transport, it was inferred that the differentially expressed transcripts could be probable objectives or promising targets for sorghum improvement under limited N fertilizer through marker-assisted selection.

To explore native genetic variation in nitrogen use efficiency, diverse germplasm panels of sorghum in field and glasshouse were studied under CINTRIN (Cambridge-India Network for Translational Research in Nitrogen) project. The researchers and scientists are evaluating a diverse set of almost 250 sorghum accessions (including parents of backcross-derived nested association mapping (BCNAM) populations; biparental mapping populations, etc., along with accessions from different countries such as Nigeria, China, the USA, Lesotho, Ethiopia, and Mali). The trial was laid in an alpha-lattice split-plot design with three replications per genotype per N dose (with three doses of 0% N, 50% N, and 100% N of recommended nitrogen (90 kg per hectare) at ICRISAT, Patancheru. The trial was laid with 15 cm × 75 cm spacing between plants in a row and between rows, respectively, involving 60 diverse sorghum accessions adopted for short-day conditions (Fig. 12.5). The preliminary results showed the native variation to N response among accessions with possibility of identification of accessions with variable N response.

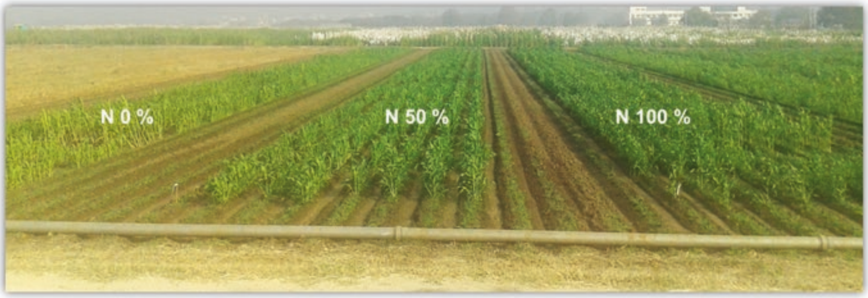

Fig. 12.5 Differential N response of sorghum accessions in field evaluation at ICRISAT-HQ, Patancheru, India, during post-rainy season of 2016–2017

12.3.3 Aluminum (Al) Tolerance

One of the constraints for the sorghum crop productivity in the tropics and subtropics, especially in West Africa, is the acidic soils (Wang et al. 2014a, b). The plants or the crops growing under the Al toxicity exhibit stunted growth and are often susceptible to drought (Marschner 1991; Kochian et al. 2004; Wang et al. 2014a, b). A single gene (AltSB/SbMATE) controls the Al tolerance in sorghum (Magalhaes et al. 2004) that has been mapped to sorghum chromosome 3. However, Magalhaes et al. (2007) have identified a gene coding for aluminum-activated citrate transporter via positional cloning, and also the markers from the similar region have been used by sorghum breeders to introgress favorable SbMATE alleles in susceptible sorghum genotypes (Anami et al. 2015).

12.3.4 Heat Stress

Air temperatures have been warming in most of the major cereal cropping regions around the world in the past decades (Lobell and Gourdji 2012). The risk of complete crop failure due to sterility during the critical reproductive period of heat stress was reported by (Teixeira et al. 2013). The average yields were ≤ 1.0 t ha^{-1} due to negative impacts of these stresses. Moreover, climate change factors are projected to impact the sorghum yields considerably especially for short duration of high temperature (above optimum) (Prasad et al. 2008). For growing sorghum, the mean optimum temperature range for grain sorghum is 21–35 °C for seed germination, 26–34 °C for vegetative growth and development, and 25–28 °C for reproductive growth (Maiti 1996). Sorghum-producing regions often experience daytime/nighttime temperatures of >32 °C/22 °C (Prasad et al. 2006). The effect of high-temperature stress causes significant decrease in sorghum grain yields as reported by Prasad et al. (2006). For grain sorghum, the dry matter and seed yields were maximum at 27 °C/22 °C (daytime/nighttime temperature), and temperatures above 33/28 °C during early stages of panicle development induce floret and embryo abortion (Downes 1972). Several reports have shown decrease in seed-filling duration, resulting in smaller seed size and lower seed yields due to high temperatures (Chowdhury and Wardlaw 1978; Kiniry and Musser 1988). In a study conducted by Prasad et al. (2006), season-long (from emergence to maturity) effects of a range of high temperatures (HT) >35/25 °C on physiology, growth, and yield of grain sorghum hybrid DK-28E were quantified, and also due to HT (≥36/26 °C), there was significant decrease in the seed set, seed number, seed size, seed-filling duration, and seed yields when compared with optimum temperature (OT) (32/22 °C). At the seedling stage in terms of poor emergence, plant death and reduced plant stands, sorghum was observed to be sensitive (Kumar et al. 2011). For heat tolerance in sorghum, genetic variability was observed (Sullivan and Blum 1970; Blum and Ebercon 1976; Sullivan et al. 1977; Sullivan and Ross 1979; Jordan and Sullivan 1981).

Reports have shown the effects of high-temperature stress which are more prominent on reproductive development than on vegetative growth, and the sudden decline in yield with temperature is mainly associated with pollen infertility in many crop species (Young et al. 2004; Zinn et al. 2010). A set of 18 diverse sorghum genotypes were used to explore genotypic variation in high-temperature tolerance where plants were grown in a controlled environment facility under four conditions ranging in maximum temperatures from 32 °C to 38 °C but had similar minimum temperature at 21 °C and relative humidity throughout the day ranged between 52% and 94%. Results have shown that high temperature significantly accelerated development and reduced plant height but had no consistent effect was observed on the leaf area per plant. In vitro studies conducted on pollen germination percentage and seed set percentage were significant for all genotypes. Pollen germination percentage and seed set percentage were observed to be highly correlated, for subset of six genotypes, and seed set percentage in controlled environments correlated well with that in field experiments that experienced similar temperatures around anthesis. These results indicated that seed set percentage could be a useful phenotypic screen for high-temperature tolerance (Nguyen 2014). These observations indicated that seed set percentage could be a useful phenotypic screen for high-temperature tolerance in sorghum. Screening for seed set percentage in plants subjected to high temperatures around anthesis could provide a phenotypic screen for high-temperature tolerance that could be an implementation in crop improvement programs.

12.4 Genomic Interventions for Biotic Stress Tolerances in Sorghum

Various biotic stresses affect sorghum leading to a severe reduction in productivity and production in various production systems (Kumar et al. 2015). For overcoming these biotic stresses, combination of genetic and management practices could be an effective means to alleviate the problem up to some extent, but the development of insect-resistant high-yielding varieties for farmer cultivation had not been commenced effectively. One reason for this lacuna could be lack of knowledge on inheritance of agronomic and morphological characteristics allied with insect resistance and yield of the crop (Sharma et al. 2005; Riyazaddin et al. 2015). For reduction of plant biotic stress from insect attacks, late planting could be an option (Li et al. 2007). Various diseases such as anthracnose, charcoal rot, etc., have been reported in several years affecting the sorghum productivity.

Globally, sorghum is reported to be damaged by over 150 insect species triggering the predictable annual loss of more than US$ 1000 million (Sharma et al. 2003). For sorghum productivity and production, the major biotic constraints are insects and pests such as shoot fly (*Atherigona soccata*) that is often considered to be the major yield limiting factor causing damage to the late sown sorghum crop. In addition, stem borer and aphids are insect-pests causing severe crop damage at later growth stages. The following section briefly discusses the major biotic stresses for sorghum production.

12.4.1 Shoot Fly

Grain and fodder yield losses in sorghum are mostly due to shoot fly infestation which results in decreased plant stand of the crop. The global yield loss due to shoot fly has been reported to be approximately over than US$ 274 million (Sharma 2006). The estimated losses due to this pest have been reported to reach as high as 86% for grain and 46% for the fodder yield (Syed et al. 2017). The yield loss in sorghum due to shoot fly occurs after the emergence of sorghum seedlings between the first and fourth week. The infestation of shoot fly occurs by oviposition on the leaf surface of the third and sixth basal leaves of the seedlings. The major loss was observed in the plant stand and the grain yield due to shoot fly increase on account of delayed planting exclusively in high-yielding cultivars of sorghum (Rai et al. 1978).

By the use of resistant varieties, seed treatment with systemic insecticides, planting in time, and need-based foliar spray applications during the seedling stages, the yield losses due to shoot fly can be evaded to a major extent (Sharma 1985). Also one of the major effective means is to have host plant resistance for the shoot fly populations keeping the poor farmers benefitted from the use of costly insecticides for shoot fly damage in the semi-arid zones (Sharma 1985; Sharma 1993; Riyazaddin et al. 2015).

Improvement in genetic makeup of sorghum crop considering the economic importance of this pest is a major objective of many sorghum breeding programmers. For a better understanding of resistance inheritance, QTL identification and the linked markers are important for successful introgression of the identified QTLs through marker-assisted breeding. Past reports and studies on sorghum shoot fly resistance recommend quantitative nature of the trait (Sajjanar 2002; Folkertsma et al. 2003). A total of 29 QTLs for 5 component traits of shoot fly resistance were identified by Satish et al. (2009) in a 168 RIL mapping population derived from the cross 296B × IS18551 with a varying degree of phenotypic variation. Screening of 32 sorghum genotypes for shoot fly resistance has been accomplished, of which 16 genotypes were found to be resistant to shoot fly dead hearts (Prasad et al. 2015). Introgression of four validated QTLs imparting resistance for shoot fly at ICRISAT, governing major component traits such as dead hearts incidence, leaf trichome density, reduced oviposition, and leaf glossiness, was done into two elite genetic backgrounds of BTx 623 and 296 B through MABC (Ramu et al. 2010). The research aimed at discovering the genetic basis of resistance into QTL, using replicated phenotypic data sets obtained from 4 test environments, and a 162 microsatellite marker-based linkage map constructed using 168 RILs of the cross 296B (susceptible) × IS18551 (resistant) (Satish et al. 2009). Similar research was done by Aruna et al. (2011) for shoot fly resistance and associated traits that detected 25 QTLs (five each for leaf glossiness and seedling vigor, ten for dead hearts, two for adaxial trichome density, and three for abaxial trichome density) in individual and across environments. The QTLs identified in these researches will enable marker-assisted breeding for shoot fly resistance in sorghum in future breeding programs, and efforts have already been in progress toward this direction at ICRISAT.

12.4.2 Stem Borer

In different sorghum-growing regions all over the world, several species of stem borer attack were observed (Nwanze 1997) among which spotted stem borer (*Chilo partellus)* is predominant in Asia and eastern and southern Africa. Usually three types of stem borers that attack sorghum include the spotted stem borer, African maize stalk borer, and the African pink stem borer. Several strategies and methods are available for the management of stem borer as mentioned earlier besides chemical insecticides, such as biological control like introducing parasitoids (*Cotesia flavipes*) (Khan et al. 2003; Tende et al. 2005). However, there is no such treatment which could completely eradicate the stem borer damage, as biological methods are laborious and time-consuming and are not effective in the long run when already the damage had happened (Mailafiya et al. 2009). Chemical insecticide control, if applied before the damage, had inflicted on the crop as the most effective measure for stem borer control. But usage of chemical insecticides is too expensive and out of the reach of poor farmers. A viable option for the farmers would be the host plant resistance for the insect pest management in sorghum and also other cereals that will be cheaper, environmental friendly, and mostly compatible to other pest control strategies (Tadele et al. 2011). Indian national sorghum improvement program (whole world population screening) and International Crops Research Institute for the Semi-arid Tropics (ICRISAT) had screened over 30,000 world germplasm accessions for spotted stem borer resistance (Singh et al. 1968; Pradhan 1971; Jotwani 1978; Taneja and Leuschner 1984; Sharma et al. 1992, 2003). The studies done by Sharma et al. (2003) on the effect of spotted stem borer damage on fodder quality in sorghum resulted in the assessment of the losses associated with stem borer in fodder yield and quality in sorghum. The study also revealed a very significant outcome of identifying a dual-purpose (fodder and grain) cultivar by the farmers for the stem borer-resistant sorghum genotypes (Sharma et al. 2003).

Stem borer resistance is a quantitative trait with little heritability (Singh et al. 2011). Inheritance additive genes were reported to be important for stem borer resistance (Karaya et al. 2009). When selections for *B. fusca* and *C. partellus* resistance were implemented, multiple traits such as exit holes, leaf feeding, stem tunneling, and dead heart were considered (Tadele et al. 2011). The factors in the cytoplasm of the nuclear genes and the maintainer lines influence the stem borer resistance (Sharma et al. 2007). In both the restorer and the male sterile line, high level of resistance is the prerequisite for production of stem borer-resistant hybrids (Dhillon et al. 2006). Inheritance of the markers and quantitative traits recognized can be used to select complex traits by enhancing the quantitative trait loci mapping (Bernardo 2008). For the damage due to stem borer in sorghum, genetic linkage maps are essential for resistance/tolerance (Sally et al. 2007). In cereals, many distinct QTLs for stem borer and agronomic traits had been mapped. For the resistance to European corn borer-stem tunneling, QTLs were mapped in RILs of “B73” × “DE811” (Krakowsky et al. 2004).

12.4.3 Anthracnose

One of the destructive fungal diseases in sorghum that causes high-yield losses is anthracnose, caused by *Colletotrichum sublineolum*. Anthracnose was first reported in sorghum from Togo in 1902. This disease presently reported worldwide (Bergquist 1973; Frederiksen 1984; Heald and Wolf 1912; Hsi 1956; Miller 1956; Pastor-Corrales and Frederiksen 1980; Porter 1926; Sundaram et al. 1972; Tarr 1962). The strategies for increasing production against fungal pathogens, genetic engineering, and classical breeding for the traits conferring tolerance and resistance could be a precise approach for decreasing the losses caused by them. All the areal parts of sorghum including tissues can be infested by anthracnose (Erpelding 2010). On all of the above ground tissues of the sorghum plant, anthracnose infection can be detected that includes seed, panicle, stalk, and leaf (Hess et al. 2002; Thakur and Mathur 2000). For anthracnose control, the most cost-effective measure is genetic resistance (Rezende et al. 2004).

In sorghum, many diverse sources of anthracnose resistances have been identified and were already mapped by several research groups from biparental crosses on chromosome 6 using an F5 mapping population (Klein et al. 2001). Another research by Mohan et al. (2010), QTL identification with a biparental mapping population of 168 F7 lines, was reported. Also Singh et al. (2006) on SBI-08 has identified markers for a recessive anthracnose resistance allele from 49 F8 inbred lines from mapping population. One more population association study for anthracnose resistance was performed by Upadhyaya et al. (2013) on sorghum mini-core collection (Upadhyaya and Gowda 2009). A RIL population was produced of 117 inbred lines by a study done by Burrell et al. (2015), and a total of 619 SNP and three microsatellite markers were generated for creating a genetic map for QTL analysis. This phenotyping study for anthracnose symptoms confirmed similar results for identified QTLs on chromosome 5, with the research of Cuevas et al. (2014) and Perumal et al. (2009). For detection of the resistance genes, molecular markers and QTL analysis play important role in carrying out marker-assisted selection for few fungal diseases. A recent study conducted by Patil et al. (2017) identified QTLs with different variable levels of resistance across all the tested environments. For marker-assisted introgression of confirmed anthracnose resistance genotypes into elite sorghum inbreds, single nucleotide polymorphisms linked to these loci will be very informative and a useful tool for future research (Patil et al. 2017).

12.4.4 Charcoal Rot/Stalk Rot

Charcoal rot also known as stalk rot is another major disease that occurs in sorghum-growing areas across the world. The charcoal rot is caused by *Macrophomina phaseolina* that affects the grain sorghum plant, as a result the sorghum panicle fails to fill the grain properly. In severe charcoal rot, the plants even may lodge in the later part of the season. Also fungal structures can be observed in the affected tissues that appear dusted with black pepper. The charcoal rot control management can be done by avoiding moisture stress, by balancing nitrogen and potassium fertility levels, and by growing drought-tolerant cultivars as well lodging resistant varieties, which could be some of the best means for its control. Modern biotechnologies have proved to be boon for such severe diseases as it provides DNA-based markers that could be genetically associated with economically important traits.

A very recent research done on charcoal rot by Reddy et al. (2008) had identified QTLs for the charcoal resistance in sorghum. This study had grown a F9 population consisting of recombinant inbred lines (RILs), derived from IS 22380 (susceptible) and E36–1 as resistant check in two locations of Dharwad and Bijapur in Karnataka, India. At both locations nine QTLs were identified for the component traits of charcoal rot disease (Dharwad, five QTLs, and Bijapur, four QTLs). The identified QTLs can further assist in marker-assisted selection (MAS) for charcoal rot resistance in sorghum. Another research done by Borphukan (2017) had revealed three QTLs for the charcoal or the stalk rot disease in sorghum. The study was carried out on the mini-core set of 242 sorghum accessions at ICRISAT and was evaluated with 2 charcoal rot check cultivars SPV 86 (susceptible) and E36–1 (resistant) under charcoal rot sick plot condition at MARS, Dharwad harboring charcoal rot resistance QTLs (qCr1, qCr2, qCr3). All the identified QTLs were found to be present in six sorghum accessions, i.e., IS4515, IS13549, IS29582, IS25301, IS12735, and IS23514. Another interesting observation was made that three resistant accessions (IS19389, IS17941, IS29233) and two moderate resistant accessions (IS1212 and IS32439) were found to carry the three qCr combinations.

12.4.5 Grain Mold

Another major constraint to sorghum productivity is the grain mold disease. This disease is also one of the most widespread diseases worldwide. Its effect is mostly observed in short duration hybrid cultivars and varieties, mostly grown in rainy season under humid conditions. The yield production loss due to this disease ranged from 30% to 100% depending on the cultivars, weather conditions, etc. (Singh and Bandyopadhyay 2000). However, exact estimate of the losses is difficult since it involves assessment from production to marketing and final utilization of the grain. The first visible symptoms of grain mold disease are pigmentation of the lemma, palea, glumes, and lodicules. The symptoms could be highly variable depending on the fungus involved at grain maturity stage. QTLs were reported with 130 markers including 44 SSRs and 85 AFLPs. Klein et al. (2001) reported that five QTLs for grain mold disease with 10 and 23% of the phenotypic variance in sorghum. In another glasshouse and field experiments, few QTLs were identified for grain mold disease for 242 sorghum mini-core accessions with 14,739 SNP markers (Upadhyaya et al. 2013).

12.5 Future Prospects

In the present era, data management and new genetics, genomics, statistics, and molecular resources, tools, and technologies have a great potential to enhance the efficiency of sorghum breeding program. The wide collection of germplasm, genetic, genomic, and breeding information/resources such as recent advancement in NGS, high-throughput phenotyping, next-gen breeding populations will enhance the rate of genetic gain in sorghum. Sorghum research community has access to large genetic (germplasm with unique traits) and genomic (SSRs, SNPs, high-density genetic maps, genome sequence) resources, and many QTLs/candidate genes associated with agronomic and stress tolerance traits are known in sorghum. The exploitation of a vast amount of untapped natural (primary, secondary, tertiary gene pools) and induced (TILLING, BCNAM, mutant populations, transgenics, etc.) genetic diversity could help sorghum improvement programs by mining alleles and controlling various biotic and abiotic stress tolerance. Rapid development of NGS technologies will further enhance identification of candidate genes and SNPs. The powerful combination of high-throughput genotyping and phenotyping could lead to molecular marker development and deployment for various biotic and abiotic stress tolerance traits to expedite the breeding cycle resulting in enhanced rate of genetic gains. The present era of research demands further advancement in sorghum via genetic engineering and gene transfer technologies for integration of desirable traits (without variation in cultivated gene pool) into the sorghum genome. Already many such reports are present in case of crops such as rice, wheat, and maize which has led to the development of several improved cultivars and advanced lines that show greater yields, possess good grain quality, and minimize damage caused by pests and diseases. Improvement of sorghum with enhanced nutrition value combined with biotic and abiotic stress tolerance will at the end enhance economic benefits to the farmer and lead to augmentation of the quality and production in the coming years. The integration of these new tools along with new generation breeding populations will further help accumulating the required information to develop and deploy genomic selection for sorghum improvement. For all these initiatives, a greater investment from public/private organizations with well-defined partnership with farming community is the only way ahead.

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