

Chapter 5

Genomic Designing for Biotic Stress Resistance in Sorghum



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Abstract Sorghum (*Sorghum bicolor* (L.) Moench) is an immensely valuable staple cereal crop across semi-arid tropical regions of the world and is regarded as a nutritionally potential crop compared to other cereals with high fibre content, minerals and slow digestibility. A multitude of bacterial, fungal and viral pathogens and several insect pests cause significant losses in yield and quality of sorghum. Management of these biotic stresses using chemicals is quite expensive and environmentally not sustainable. Developing host-plant resistance and use of resistant cultivars has great promise in this direction. Repository of genetic resources and the wild gene pool in sorghum that harbor many biotic resistant genes serve as a rich source to develop resistant cultivars. Crossing programs involving several resistance sources resulted in many resistant varieties, hybrids and parents. The genetic barriers between wild and cultivated sorghum species are still challenging to transfer resistant genes. However, with the recent advances in genomic tools, next generation sequencing/re-sequencing technologies, genetic engineering, more genomic data is being utilized in the sorghum breeding programs. These advanced molecular tools have helped to unravel the genetic architecture and provide a deeper understanding of the marker-trait associations. A maximum number of individuals in the mapping population coupled with large-scale genotyping with markers like SNPs would capture more recombination events, leading to high resolution of QTL

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mapping. Marker-assisted selection can now be efficiently used for pyramiding multiple resistance genes/QTLs which can accelerate the varietal development process, resulting in durable resistance with great impact on the sorghum yield stability and sustainability. This chapter provides an overview of biotic stresses in sorghum, their impact, various breeding strategies and genomics assisted tools in prospecting sorghum biotic stress resistance besides highlighting the recent concepts and future perspectives for genomic designing.

Keywords Sorghum · Biotic stresses · Nutritionally potential · Host-plant resistance · GWAS · QTL

5.1 Introduction

Sorghum (*Sorghum bicolor* (L.) Moench), the fifth major cereal crop of the world with a small genome size of 750 Mbp, is a native of Africa and possesses enormous genetic potential as a food crop, especially in disadvantaged marginal situations of the world human habitats (Paterson et al. 2009; Zhang et al. 2017b). It is known to be grown since five thousand years and as a crop of the semi-arid regions, it is being utilized as food and forage for the cattle. Much recently this crop has sustainably prospected for biofuel manufacturing (Calvino and Messing 2012). The food security necessitates a deeper understanding of the food production dynamics in the environmentally challenging situations where sorghum is being cultivated (Mundia et al. 2019). The factors that significantly limit sorghum production comprise adverse weather, poor soil fertility and most importantly the pests and diseases. Insect pests and diseases significantly affect crop yields, grain quality, marketability and its utilization as food and fodder (Savary et al. 2012) which in turn influence the food supply, if measures are not taken (Reynolds et al. 2016). The yield loss in sorghum due to biotic stresses covering all stages is anywhere between 30 and 100 % (Singh and Bandyopadhyay 2000). Global sorghum production at about 57.50 million tons during 2019–20 is expected to increase by 3.94% to meet the demand (Miller magazine 2020). Developing sorghum cultivars resistant to various biotic stresses is critical to sustaining its production to meet the present food, fodder and industrial requirements. Deployment of resistant cultivars to overcome biotic stresses can augment the solution for low productivity of cultivars. Knowledge of the genetic resources/gene pool of sorghum as the source of genes for stresses is crucial to develop biotic resistant cultivars (Kumar et al. 2014). Owing to the faster evolution and development of counter-resistance genes in pathogens and insect-pests to evade the host resistance, it is highly challenging to develop durable, long-lasting resistance through conventional approaches (Witcombe and Hash 2000). An integrated approach involving plant breeding and genomics tools could increase the efficiency and precision of resistance breeding, this has to happen on sustainable pace across different tropical and sub-tropical situations (Perez-de-Castro et al. 2012). The availability of mapping populations, molecular

markers and genetic maps in sorghum over the last two decades offered ample opportunities for the identification of genomic regions/quantitative trait loci (QTLs) associated with traits of interest, especially those associated with biotic stresses. The modern molecular tools can achieve introgression of several resistant genes/QTLs into a single cultivar through molecular breeding strategies. Marker assisted selection (MAS) has enhanced the selection efficiency in some of the important traits related to resistance against insect pests and pathogens (Dormatey et al. 2020).

Functional genomics tools coupled with diverse genetic backgrounds having broad resistance can be used to provide critical insights into the biotic stress responses (Cuevas et al. 2019). Indeed, the relevance of the sorghum functional genomics is increased with the advent of next-generation sequencing techniques (Paterson et al. 2009). Functional genomics along with the developments in genome sequencing, QTL mapping, RNA-sequencing, and bioinformatics allow a deeper understanding of the genetics of resistance both in plant and pathogen as well as insect pests (Andersen et al. 2018). The RNA-interference (RNAi) in imparting resistance to biotic stresses is becoming practically relevant in sorghum and other millets due to affordability of the technology (Banerjee et al. 2017; Majumdar et al. 2017; Zhang et al. 2017a). Transcription factors (TF), the proteins crucial in governing transcriptional regulation during the entire crop period, can function as switches to control the expression of genes involved in mediating biotic stress resistance. Characterization of transcription factor genes critically involved in plant stress responses and their introgression is vital for enhanced biotic stress resistance in sorghum.

The biotic stress management systems depend on various control approaches such as genetic, physical, chemical, cultural and biological, among others. However, the use of stress-resistant varieties can lead to enhanced ecological fitness, reduced pesticide usage and sustainable production system, resulting in increased yields and grain quality/end-use traits (Singh et al. 2004a). A multidisciplinary and multipronged approach with synergistic integration of morphological and molecular approaches i.e., plant breeding in combination with genomics tools would accelerate and maximize the efficiency of breeding programs for developing biotic stress resistance in sorghum (Dormatey et al. 2020).

5.2 Different Biotic Stresses

Sorghum is affected by various biotic factors including multiple insect-pests, diseases and parasitic weeds that cause significant economic losses.

5.2.1 Major Diseases of Sorghum

Major diseases of sorghum are grain mold, anthracnose (*Colletotrichum sublineolum*), ergot (*Claviceps sorghi* and *C. africana*), downy mildew (*Peronosclerospora sorghi*), sorghum rust (*Puccinia purpurea*), charcoal rot/stalk rot (*Macrophomina phaseolina*), bacterial leaf spot (*Pseudomonas syringae* pv. *syringae*), leaf blight (*Helminthosporium turcicum*) and head smut (*Sporisorium reilianum*). *Striga* spp., a parasitic weed is one of the most devastating constraints that can cause a cent per cent yield loss under severe infestation (Esele 1995).

5.2.1.1 Grain Mold

Grain mold is the most devastating disease of sorghum with global distribution. More severe in the *kharif* season, especially, in white-grain sorghum, which is being grown widely in Asia and Africa for food. Grain mold is less severe on colored grain sorghum being grown widely in United States of America (USA), Argentina, Australia and Mexico for feed purpose. It is a complex disease caused by more than 40 pathogenic and opportunistic fungi from several genera, including the most common species *Fusarium thapsinum* (Klittich et al. 1997; Cuevas et al. 2019). *Fusarium* spp., *Alternaria* spp., *Curvularia* spp. and *Colletotrichum* spp. were the most principal fungi reported in grain mold (Williams and Rao 1981; Navi et al. 2005). The disease develops with the infection and colonization of spikelet followed by grain colonization leading to the deterioration of seed (Bandyopadhyay et al. 2000). Fungi secrete enzymes that degrade starch in endosperm and germ tissues (Hodges et al. 2000). A devastating effect of grain mold on grain yield, quality, market value and eventually on the grain-based products with an annual loss of US\$ 50–80 million was estimated in India (Das 2019).

5.2.1.2 Anthracnose

Anthracnose caused by *Colletotrichum sublineolum* Henn. is one among the most economically damaging sorghum diseases that affect leaves, stems and grain, with significant grain yield reduction over 50–86% (Cota et al. 2017). An estimated grain yield loss of more than 50% was observed in susceptible sorghum cultivars under severe anthracnose epiphytotic in Georgia (Harris et al. 1964). The disease gets aggravated under warm and humid conditions (Tsedaley et al. 2016). Symptoms include the development of small spherical spots on leaves and leaf midribs with red, orange, purple or tan colored wide margins having straw-colored centers. In case of disease severity, the spots increase in number and conjoin covering the entire leaf surface and stem leading to premature plant death. In the centers of the spots, small black fruiting bodies (acervuli) develop (Tesso et al. 2012). A direct

negative impact on grain yield can be envisaged as the infection in later stages of development, is seen on the rachis, panicle branches and seeds.

5.2.1.3 Ergot or Sugary Disease

Ergot is caused by the fungi of the genus *Claviceps*, i.e., *Claviceps sorghi* or *Sphacelia sorghi*. Over 40 species of *Claviceps* have been reported, major include *C. sorghicola*, *C. africana* and *C. purpurea* (Pazoutova and Frederickson 2005). The infection starts with the sclerotium production within the floret and only the ovaries are infected. Ergot infects unfertilized ovaries individually within a panicle. Male sterile lines are highly susceptible. Severe infection is seen under high rainfall, high humidity, cloudy weather during anthesis and in cool night temperature conditions. The two noticeable signs of the disease are droplets of honeydew oozing from infected florets and the growth of fungal sclerotia. The hard textured sclerotia developed from sphacelia protrude few millimeters outside the glumes. The major threat from ergot is the infection and contamination of the harvested grains by toxic alkaloids present in the sclerotia (Wegulo and Carlson 2011). Major types of ergot alkaloids produced are clavine alkaloids, D-lysergic acid and its derivatives, and ergopeptines which cause a group of symptoms called “ergotism” (Hulvova et al. 2013).

5.2.1.4 Downy Mildew

Downy mildew of sorghum is caused by *Peronosclerospora sorghi*. The disease is manifested as downy whitish growth on the lower leaf surface followed by whitish streaks on both the leaf surfaces. Tissues alongside the white streaks slit later resulting in leaf shredding. Primary infection of the disease is through oospores present in the soil, mycelium in seeds and secondary infection is through air-borne sporangia. Crop rotation with other crops viz., pulses and oilseeds and removal of the infected plants can prevent the secondary spread of the disease (Tesso et al. 2012).

5.2.1.5 Rust

Sorghum rust caused by *Puccinia purpurea*, is of significance as it predisposes sorghum to other diseases such as stalk rot. The disease is manifested as small reddish-brown specks on the lower leaf surface and pustules (uredospori) on both the leaf surfaces as purplish spots which later rupture to release a reddish powdery mass of uredospores. Primary infection is through long cycled rust and secondary infection is by wind-born uridospores. Infection can be minimized through the destruction of the alternate host, *Oxalis corniculata* and spray of mancozeb (Hooker 1985).

5.2.1.6 Charcoal Rot or Stalk Rot

Charcoal rot caused by a soil-borne fungus, *Macrophomina phaseolina*, is a major fungal disease of sorghum worldwide with great destructive potential causing substantial losses in economic yield levels ranging between 14.2 and 46.6% (Mughogho and Pande 1983). After infection, the infected stalk will split open and consequently results in longitudinal shredding of the pith tissue into fibers and disintegration. The stem breaks down to the ground resulting in premature stem lodging that negatively affects the grain and fodder quality. The disease is primarily infected from the soil, weed hosts and can be aggravated by rain or irrigated water (Ghosh et al. 2018).

5.2.1.7 Bacterial Leaf Spot

Bacterial leaf spot is caused by *Pseudomonas syringae* pv. *syringae*. Symptoms include initial water-soaked lesion on the lower leaves which grow and mature, and become elliptical to circular developing red or brown margins. As lesions dry, the centers become light-colored. Most commonly found in the spring season since it is dispersed by rain and wind and becomes insignificant in summer seasons (Te-Beest et al. 2004).

5.2.1.8 Leaf Blight

Causal organism of this disease is *Helminthosporium turcicum* (Syn. *Exserhilum turcicum*). Yield losses can approach 50%. Symptoms of the disease are manifested as small reddish or tan spots that can enlarge to long elliptical reddish-purple or tan lesions of 12 mm wide and 2.5–15 cm long. Sporulation of the fungus on lesions often gives them a dark grey or olive appearance on the surface. The fungus can survive on grasses, on residue and seeds (Lu et al. 2018).

5.2.2 Insect Pests of Sorghum

More than 150 species of insect pests infest sorghum. The key pests are shoot-fly (*Atherigona soccata*), sorghum gall midge (*Stenodiplosis sorghicola*), stem borer (*Chilo partellus*), aphids (*Rhopalosiphum maidis* and *Melanaphis sacchari*), jowar ear head bug (*Calocoris angustatus*), shoot bug (*Peregrinus maidis*), red-headed hairy caterpillar (*Amsacta albistriga*) and ear head caterpillar (*Helicoverpa armigera*) causing significant damage to the crop (Sharma et al. 2006).

5.2.2.1 Shoot-Fly

The shoot-fly (*Atherigona soccata* Rondani) is one of the prominent threats for sorghum production in Asia, Africa and American continent (Sharma et al. 2003). Sorghum shoot-fly, the most devastating pest, alone is responsible for 5% loss out of 12% total insect losses. Grain yield reduction of about 50% (Jotwani et al. 1979) and a still more devastating damage with loss up to 90% was reported (Jotwani et al. 1970). High susceptibility is seen in the early stages of crop growth (5–25 days), especially in the late sown crop during rainy season, whereas, the early-sown crop is more affected during the post-rainy season (Mohammed et al. 2016). Female shoot-fly lays eggs singly on the surface of the leaf, parallel to the mid-rib. The larvae cut the growing point of the apical shoot resulting in a dead heart symptom. Larvae feed on the decaying tissue which may lead to seedling mortality and the crop gets damaged within 1–4 weeks after seedling emergence, present a rosette appearance and fail to produce any grain (Mohammed et al. 2016). Pesticides are being used to control shoot infestation in sorghum crop (Sharma et al. 2007).

5.2.2.2 Sorghum Gall Midge

Sorghum gall midge (*Stenodiplosis sorghicola* Coquillett) is an ubiquitous damaging pest of grain sorghum all over the globe (Young and Teetes 1977). A crop loss of 10–15% was reported and in severity, this can cause cent per cent damage to developing kernels in all the sorghum growing areas (Sharma and Teetes 1995). Eggs hatch and feed on the ovaries resulting in chaffy grains. Certain varieties may be particularly susceptible to egg lay in pre-flowering spikelets (Franzmann and Vaschina 1989). Sorghum midge can be managed by uniform regional planting, such that, all sorghum varieties flower within 7–14 days or through insecticide spray at anthesis. Genetic resistance mechanism that increases non-preference of florets for sorghum midge is eco-friendly and a durable approach.

5.2.2.3 Sorghum Stem Borer

Sorghum stem borer (*Chilo partellus* Swinehoe) infestation begins from over a month after sowing. The larvae feed on the surface of leaf sheath and leaf whorls, bore into the midrib and the shoot which later feed on the internal tissues causing extensive tunnelling and results in ‘dead heart’ formation and consequent killing of young plants. Larvae also infest ear heads and cause tunneling leading to chaffy ear heads and poor grain development. Chemical control includes soil application of phorate or carbofuran at the time of sowing. Many parasitoids viz., green lacewing, ladybird beetle, spider, fire ant, reduviid bug, robber fly, black drongo, big-eyed bug, earwig, ground beetle, pentatomid bug, praying mantis, *Dicyphus hesperus* etc. are effective against stem borer. Greenleaf desmodium can also be used as a control strategy against stem borers in sorghum (Khan et al. 2006).

5.2.2.4 Aphid

Both sorghum aphid (*Rhopalosiphum maidis* Fitch) and sugarcane aphid (*Melanaphis sacchari*) are common in several sorghum growing countries (Singh et al. 2004a). The severity of aphid damage is up to 77% reduction in grain yields (Van Rensburg and Hamburg 1975). Aphids usually attack newly emerged leaves, wherein, the adult and nymphs cause the damage throughout the growing period by piercing and sucking sorghum juice which eventually slows down plant growth leading to plant death. Sorghum is reported to be a preferred host for sugarcane aphid (Bowling et al. 2016). Aphids produce honeydew in plenty on which sooty molds grow, which further hinder grain harvesting and grain quality (Wang et al. 2013). Leaf extracts from neem seed or dursban found to be effective in controlling aphids (Diarisso et al. 2005). Insecticides viz., dimethoate 30 EC and imidacloprid formulations are reported to be most effective in reducing the aphid population.

5.2.2.5 Jowar Ear Head Bug

Jowar ear head bug (*Calocoris angustatus*) is a vigorous, small yellowish-green bug that infests the crop from ear head emergence to dough stage and causes about 54–89% reduction in grain yield levels. During ear head formation, ear head bugs are usually seen covering over the ear heads. Both nymphs as well as adults suck the milky juice from ear heads or developing grains, as a consequence the grains shrink and turn black color leading to chaffy or crinkled grains. Older grains show distinct feeding punctures that reduce grain quality (Sharma 1985).

5.2.2.6 Shoot Bug

Shoot bug (*Peregrinus maidis*) is a sporadic pest of sorghum that can cause heavy damage under favorable conditions. Nymphs and adults suck the sap from young leaves and leaf sheath resulting in unhealthy plants, with reduced plant vigor and yellowing. Under severe infestation, the leaves wither from top-down and later turn reddish finally leading to plant death. The infestation generally leads to twisting of leaves and seldom of panicles emergence—collectively results in over 41% yield toll in India (Subbarayudu 2002). Deep summer ploughing, collection and destruction of larvae, crop rotation with non-host crops, timely sowing, destruction of alternate host plants, field sanitation, rogueing, early uprooting and burning of infested plants can reduce the incidence of pest.

5.2.2.7 Red Headed Hairy Caterpillar

Red headed hairy caterpillar (*Amsacta albistriga*, *A. moorei*), a polyphagous pest is highly injurious to young sorghum seedlings. Caterpillars are voracious feeders

which feed on leaves by scrapping the under surface of tender leaflets besides flowers and main stem in later stages independently, they spread across fields, which lead to severe crop damage and yield loss (Nagarajan et al. 1957). Use of light traps and digging trenches around the infested field and dusting with insecticide can reduce the pest infestation.

5.2.2.8 Ear Head Caterpillar

The adult ear head caterpillar (*Helicoverpa armigera*) is a medium-sized moth. Caterpillars feed till grain hardening stage and are covered in the inner branches of the ear. Compact panicles are more prone to heavy damage and damaged ears could be easily spotted in the field by their chalky appearance (Bora et al. 1994).

5.3 Genetic Resources of Resistance Genes

The sorghum germplasm resources can stand rounds of intense selection to meet diverse requirements of plant breeding due to its rich genetic diversity that stems from five basic races - *Bicolor*, *Guinea*, *Caudatum*, *Kafir*, *Durra* and 10 intermediate races that include -*Guinea-bicolor*, *Durra-bicolor*, *Caudatum-bicolor*, *Guinea-caudatum*, *Kafir-bicolor*, *Guinea-kafir*, *Guinea-durra*, *Durra-caudatum*, *Kafir-caudatum*, *Kafir-durra* (Harlan and de Wet 1972; Venkateswaran et al. 2019). The rich genetic diversity in the gene pool 1 (GP-1) and gene pool 2 (GP-2) and their cross-compatibility with *Sorghum bicolor* have led to the development of successful hybrids. Most significantly, *S. bicolor* subsp. *verticilliflorum* and *S. propinquum* have contributed for yield per se and *S. halepense* has contributed genes for crop duration (Dweikat 2005; Aruna and Cheruku 2019). Wild species, harbouring genes, which are resistant against striga are *arundinaceum*, *virgatum* and *verticilliflorum* (Cox et al. 1984; Bramel-Cox and Cox 1988). Other potentially useful traits in sorghum's GP-1 and GP-2 include *S. bicolor* subsp. *drummondii* for allelopathic properties and resistance to ergot and nematodes, and *S. halepense* conferring resistance to multiple pests (Dweikat 2005; Baerson et al. 2008). Further, the gene pool 3 (GP-3) of sorghum has enormous potential in gaining grain yield advantage through introgression of specific genes and it is envisaged that the diversity in GP-3 would be of particular use in breeding sorghum for climate change eventualities and dreaded insect pests of sorghum (Venkateswaran 2003; Kamala et al. 2009) (Fig. 1).

The concept of core collection facilitates thorough characterization of accessions for various traits of interest and thereby maximizing the use of the germplasm. The core collection consists of a subset of accessions from the entire collection, capturing most of the species diversity. Further, Upadhyaya and Ortiz (2001) postulated the concept of mini core collection with 10% core collection accessions. Repeated evaluation of the reference collection, core collection and mini-core

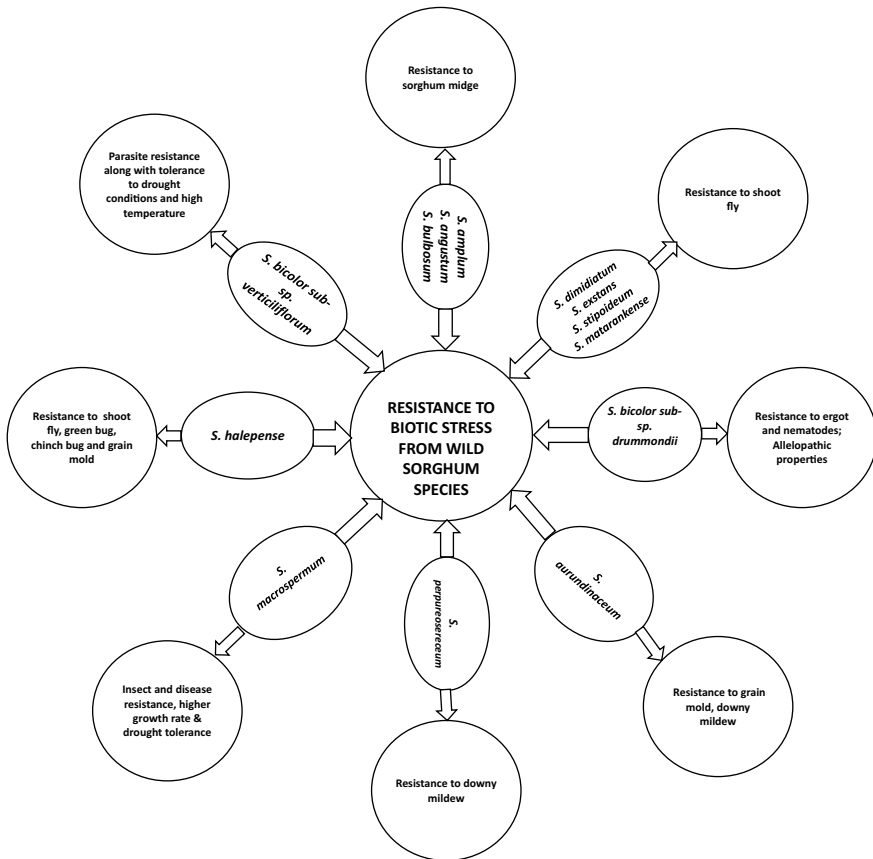


Fig. 5.1 Resistance to biotic stress from wild sorghum species. The genus *Sorghum* consists of 25 diverse species, among which few wild species confer resistance to major pests and diseases of sorghum. *S. bicolor subsp. verticilliflorum* gives high yield along with tolerance to drought conditions and high temperatures (Bramel-Cox and Cox 1998; Rich et al. 2004). *S. bicolor subsp. drummondii* has allelopathic properties to ergot disease and nematodes (Mojtahedi et al. 1993; Tsukiboshi et al. 1998). The species *S. amplum*, *S. angustum*, and *S. bulbosum* are a source of resistance sorghum midge (Sharma and Franzman 2001). *S. dimidiatum*, *S. extans*, *S. stipoides*, and *S. matrankense* are a source of resistance to major pest of sorghum, shoot fly (Nwanze et al. 1995; Kamala et al. 2009). *S. perpureosereceum* confers resistance to downy mildew (Sharma 2010). *S. halepense* is resistant to shoot fly, green bug and chinch bug (Nwanze et al. 1995; Dweikat 2005). *S. aurundinaceum* is resistant to grain mold and downy mildew (Mohan et al. 2008). *S. macrospermum* has resistance to many pests and diseases along with higher growth rate and significant aboveground Dhurrin content under drought conditions (Kuhlman et al. 2008; Cowan et al. 2020)

collections of sorghum germplasm resulted in the identification of accessions useful in breeding for various biotic stresses. These include, **Grain mold**: White-grained four guinea race accessions and a set of 50 sorghum mini core accessions have been reported to be resistant to grain mold (Sharma et al. 2010). **Anthracnose**: a set of 13 accessions including IS10302, IS19153, IS20956 and IS24218, recorded minimal mean disease scores (Sharma et al. 2012). **Leaf blight**: IS2906, IS18417, IS18425, IS18758, IS19667 and IS19669 (Reddy et al. 2004); besides a set of 27 accessions of mini core recorded resistance with a mean disease score of 2 (Sharma et al. 2012); **Rust**: IS3413, IS13896, IS18417, IS21454 and IS29016; IS473, IS23521, IS23684, IS24503, IS26737 and IS33023 with mean disease severity of 3.8% (Reddy et al. 2004; Sharma et al. 2012); **Downy mildew**: IS3547, IS20450, IS23992, IS27697, IS28449, IS28747, IS30400 and IS31714, (Reddy et al. 2004; Sharma et al. 2012); **Potyvirus spp.**: IS7679 and IS20740 (Seifers et al. 2012); Further, accessions such as IS2058, IS18758, IS3547, IS14332, IS17141, IS2333, IS14387, IS3413, IS14390, IS21454 have shown multiple disease resistance (Reddy et al. 2008; Sharma et al. 2010, 2012).

5.4 Traditional Breeding for Disease and Pest Resistance

Insect pests and diseases cause considerable loss in grain and fodder yield levels besides the quality of produce. Resistant cultivars that are genetically superior form the cheapest method for minimizing the yield toll. Breeding for host plant genetic resistance is a continuous process in terms of searching for source accessions that are resistant to ever-evolving new races of the pathogens (Singh and Bandyopadhyay 2000; Mohammed et al. 2016). Classical breeding methods such as introduction, selection, backcrossing, pedigree method, recurrent selection schemes continue to play vital roles in evolving resistant cultivars. All through the history of the plant breeding, the crop wild relatives have been the sources of resistance genes (Hariprasanna and Rakshit 2016). However, a multidisciplinary approach to utilize these crop wild relatives is critical in achieving success (Kamala et al. 2016; Ananda et al. 2020). Sorghum germplasm with rich and diverse crop wild relatives offers an excellent opportunity to improve the deficient agronomically superior cultivars/hybrids. In sorghum, wild relatives such as chaeto, hetero, stipo, and parasorghum have been potential sources of biotic stress tolerant genes (Kamala et al. 2002).

5.4.1 Traditional Breeding Research for Diseases Resistance

5.4.1.1 Grain Mold

Grain mold being a disease complex, its development mechanisms are fairly described (Waniska et al. 2001). Both major and minor genes with additive and epistatic effects coupled with significant genotype X environment (GXE) interaction have been reported (Stenhouse et al. 1997; Rodriguez-Herrera et al. 2000). Limited success in resistant cultivar development to this disease could be attributed to complex genetics, mechanisms governing resistance and high influence of the environment (Audilakshmi et al. 2011). The conventional breeding prospected 'grain hardness' to improve grain mold resistance in white-grained sorghum used for human consumption in Asian and African countries (Das et al. 2020) and this approach has been successful in developing cultivars with high yield and resistance to grain mold through an expanded systematic screening and selection in segregating progenies of specifically planned crosses (Reddy et al. 2000). The resistant sorghums belonging to the guinea race with open panicles, large glume coverage along with grain hardness need to be involved in the crosses (Reddy et al. 2000). Germplasm from Sudan and Ethiopia which possessed desirable quality with white grains as well as less susceptibility to grain mold under natural conditions was utilized in the development of variety CSV 4, which further served as restorer parent for several hybrids viz., CSH 5, CSH 6 and CSH 9 in India (Ashok Kumar et al. 2011b). Accessions such as E 35-1, CS 3541, SC 108-3, SC 108-4-8 and SC 120 continue to be parents of choice in widening the genetic base of grain mold resistance in sorghum improvement programs of India and Africa (Reddy et al. 2000; Ashok Kumar et al. 2011b).

Pedigree breeding followed by multi location testing led to the identification of many advanced breeding lines which were used to develop high yielding grain mold resistant varieties and hybrids, such as SEPON 77, M 90038 and SEPON 82 × S 34. Many grain mold resistant lines with dwarf and earliness sorghum segments, grain and glumes traits from guinea along with semi-compact heads were developed through pedigree breeding (Stenhouse et al. 1997). A grain mold resistant population was developed with white-grained, color-grained lines coupled with higher grain yielding ability into genetic male-sterility (ms3) background. Repeated half-sib family selections and cycles of random mating resulted in pinning down of several superior lines with resistance, which eventually contributed to the release of grain mold resistant varieties and hybrids in India (Ashok Kumar et al. 2011a). Germplasm sources with wide adaptability and high grain quality along with the grain mold resistance are available. Resistant lines viz., ICSB392, ICSB403, ICSB383, IS13817, IS8614, IS10646, IS25060, IS21599 and IS23585 have been used extensively in the breeding programmes (Reddy et al. 2005).

5.4.1.2 Ergot

Ergot resistant trials, with susceptible A-lines and R-lines, concerning to incidence and severity of the disease revealed Tx2737 as a popular R-line. A male-fertile accession from Ethiopia, IS8525 with high levels of resistance was considered as a potential source for host-plant resistance strategies. Five CMS-lines were crossed with five pollinator lines without fertility restorer genes, wherein, the pollinator lines on an average had low (7–10%) and the CMS female lines had very high (62–82%) ergot severities (Reed et al. 2002). Further, pollen traits such as genetic architecture, pollen quantity and pollen viability have significant correlations with the ergot resistance. The genetic correlations studied among different traits have also have pointed at possibilities of common genetic factors controlling these traits (Parh et al. 2008). Three male-sterile lines in sorghum exhibited noteworthy differences in ovary colonization rates after inoculation (Komolong et al. 2003). Further, ergot severity with high heritability behaved quantitatively and the possible effect of floral traits need to be understood, as the resistance donor was having a short, narrow stigma, least or no stigma.

5.4.1.3 Charcoal Rot or Stalk Rot

Stalk rot resistance in sorghum is associated with a delay in leaf and plant death. Different genetic control mechanisms within SC599-11E for non-senescence and charcoal rot resistance envisaged that these two forms of resistance are not different pointers of the same trait (Tenkouano et al. 1993). The component traits—internode number was associated with two QTLs on linkage group B, the length of infection associated QTL on linkage group D and two QTLs associated with per cent lodging on linkage group I (Reddy et al. 2008; Patil 2011). Stalk rot-resistant sorghum genotypes were unaffected by the pathogen-mediated yield retardation (Bandara et al. 2019). High-temperature stress decreased chlorophyll and *Fv/Fm*. Genotypes PI533946, IS26749, IS23992, RTx7000, and SC35 had the maximum *Fv/Fm* and the genotypes IS19262, SC35, PI576380 and IS27912 had resistance to both pathogens (Perumal et al. 2020).

5.4.1.4 Downy Mildew

Concerted efforts to search and characterize the resistant sources for downy mildew by using the dual approach of sandwich inoculation technique and green-house screening revealed high-level resistance to the disease in a set of six accessions viz., IS28747, IS27697, IS31714, IS28449, IS23992 and IS30400 out of 242 germplasm accessions of sorghum mini-core collection from diverse geographies (Sharma et al. 2010; Rashid et al. 2018).

5.4.1.5 Rust

Eight loci with a significant effect on rust resistance with a total phenotypic variation explained (PVE), varied from 6.8 to 42.6% (Tao et al. 1998). Of the 12 sorghum varieties screened, a local cultivar ‘Tetron’ was reported to be highly resistant with zero yield loss compared to 40% yield reduction in 97 MW 6129 (NVT11 4). Impact of this disease on seed germination was also observed (Abera and Alemayehu 2012). A set of 13 advanced breeding lines generated from a cross between UPCA-S1 and Numbu revealed significant $G \times E$ interaction on leaf rust disease severity.

5.4.1.6 Multiple Disease Resistance

Field studies have revealed that an effective screening strategy can identify resistance sources to multiple pathogens in sorghum germplasm as vast genetic diversity to individual component traits exist across its species and subspecies (Prom et al. 2012). The development of several diseases simultaneously on a susceptible sorghum grown as a mixed stand with either maize or resistant sorghum found to be a good strategy (Ngugi et al. 2001). Over 242 sorghum mini-core collection evaluated to identify resistant ones for anthracnose and leaf-blight diseases resulted in 13 accessions resistant to anthracnose and 27 to leaf blight (Kimball et al. 2019). These accessions with resistance to multiple diseases would be potential sources for sorghum disease resistance breeding programs (Upadhyaya et al. 2013a). Parental genotypes such as 234112, Bt-623, 226057 and 210903 with positive genetic combining ability (GCA) effects -Bt-623 \times Gemedi, 210903 \times 234112, 210903 \times 71708, 74222 \times 234112, 74222 \times 226057, 234112 \times 71708, 226057 \times 214852 and 226057 \times 214852 with positive specific combining ability (SCA) effects for grain yield and the desirable families: 174222 \times 234112, Gemedi \times 71708, Bt-623 \times 234112, Bt-623 \times Gemedi, 226057 \times 71708, Chemedi \times 71708, and Gemedi \times 71708 with negative SCA effect and low anthracnose severity were forwarded as promising populations for resistance breeding (Mengistu et al. 2019).

5.4.2 *Traditional Breeding Research for Resistance to Insect Pests*

5.4.2.1 Shoot-Fly

Shoot-fly resistance is a complex trait, that depends on the interplay of many component traits of plant, insect and environment. Developing genetically superior resistant cultivars offers a sustainable pest management system with enhanced grain

quality (Sharma et al. 2005; Mohammed et al. 2016). Resistance is manifested in the form of non-preference for oviposition (Dhillon et al. 2006). Systematic screening and further evaluation of sorghum germplasm led to identification of resistant accessions (Sharma et al. 2014a). Use of these resistant accessions in crossing programs led to the development of several shoot-fly resistant (SFR) varieties and hybrids (Kumar et al. 2014). Shoot-fly resistant superior advanced breeding lines such as IS2122, IS18551, IS2146, IS1054, IS2312, SFCR151, ICSV705 and SFCR125 were derived from germplasm (Riyazaddin et al. 2015). Rigorous breeding efforts have evolved cultivars that are significantly tolerant to shoot-fly incidence. Germplasm after infestation by the shoot-fly recovered in varying proportions. The accessions, CSV 22 and RSV 1093 revealed high grain yield potential in addition to shoot-fly resistance, while Phule Yashoda, RSV 1235, IS 2312, and ICSV 574 were high yielding with moderate resistance (Sharma et al. 2015). Similarly, another set with 10 parents, 45 F₁'s along with their reciprocals screened for shoot-fly resistance and inferred that the genotypes ICSV 700, ICSV 25019 were useful (Mohammed et al. 2016).

The morphological traits allied with an expression of resistance/susceptibility to shoot-fly exhibited significant GCA effects. The interlard-fishmeal technique used to increase shoot-fly abundance at seedling stage of susceptible cultivars such as Swarna was effective and successful (Chamarthi et al. 2011). In a successful effort, a trait-based pedigree breeding approach was used to develop *khariif* and *rabi* sorghum grain types in both agronomically superior genotypes and genotypes with specific traits of importance. New sources of resistance such as IS923, IS5072, IS1057, IS1071, IS4664, IS1082, IS4663, IS1096, IS2394, IS5636, IS5470 and IS18369 have been mined to infuse and breed for shoot-fly resistance in sorghums (Kumar et al. 2014). A comparative study indicated that upregulation of total soluble sugar, total phenol, prussic acid and chlorophyll play a dominant role to impart resistance in the susceptible sorghum genotypes (Kumari et al. 2020; Salama et al. 2020).

5.4.2.2 Sorghum Gall Midge

Sorghum gall midge was first reported in 1953 in 'Nunaba' varieties from West Africa (Bowden and Neve 1953). Efficient management requires combining several strategies that suppress midge damage and abundance in the field. Resistance to this pest has been attributed to the traits long glumes and non-anthesis. Field tests have suggested that 'Nunaba' varieties were resistant under choice conditions in the presence of an alternative host, but susceptible in the absence of a more favorable host (Passlow 1965). Spikelet flowering time and morphology have a direct influence on the per se resistance. Genotypes that displayed resistance under no-choice conditions in glasshouse and field trials were reported to deploy an antixenosis resistance mechanism (Franzmann 1988). The mechanism of resistance to midge has been recognized as reduced egg-lay (Franzmann 1988; Sharma and Vidyasagar 1994). Midge resistant sorghum hybrids gave higher yields and greater

returns than susceptible hybrids under the same insecticidal spray regime (Teetes et al. 1986). There is little clear evidence on the exact chemical or physical components that affect the antibiosis mechanism of resistance in sorghum. Association between tannins and midge resistance is also noted (Santos and Carmo 1974; Sharma 1985, 1993). The hybrid breeding approach has been successful to achieve resistance (Boozaya-Angoon et al. 1984).

5.4.2.3 Sorghum Stem Borer

Larva of stem borer crawls and feeds on tender leaves that become folded, causing typical “shot hole” symptom. Sorghum genotype IS18573 displayed antibiosis to stem borer in terms of reduced survival and development (Kumar et al. 2006). Induced resistance in sorghum genotypes against stem borer infestation included elevated expression of peroxidase (POD), polyphenol oxidase (PPO), hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) (Hussain et al. 2014).

5.4.2.4 Aphid

Aphid has emerged as a potential threat to sorghum. Resistance to this pest was assessed by testing 23 genotypes for tolerance to antixenosis and antibiosis and was compared with the known resistant cultivar ‘TX 2783’ and the susceptible ‘KS 585’. The entries viz., AG1201, AG1301, W844-E, and DKS 37-07 expressed all three forms of resistance to aphids, while H13073 exhibited antibiosis and tolerance (Paudyal et al. 2019). Screening of a diverse set of sorghum genotypes resulted in the identification of several lines with moderate levels of resistance to aphid damage.

5.4.3 *Traditional Breeding for Resistance to Striga*

Witchweed (*Striga* spp.) infestation is an obstacle to sorghum cultivation and it inflicts both grain and biomass production. Over 20–100% yield reduction has been recorded in Asian and African countries (Ejeta and Gressel 2007; Parker 2009). Co-evolution of sorghum with striga in Africa might have resulted in inherent resistance, which is of scope as a breeding strategy (Shayanowako et al. 2018). Complex interactions between host, parasite and the physical environment have restricted the exploitation of resistance to striga (Ejeta and Gressel 2007). Several novel techniques have been employed to identify unique resistance sources to striga followed by introgression of these genes into selected cultivars with multiple resistance mechanisms. Several high yielding cultivars with striga resistance have been deployed in many African countries (Ejeta and Gressel 2007; Mbuvi et al. 2017). Over 25 sorghum accessions screened for *Striga hermonthica* were shown

resistance along with yield in Nigeria, identified SRN39, Sepon82, Danyana and SAMSORG40 as the top four resistant accessions to *S. hermonthica* (Afolayan et al. 2020). Seeds of acetolactate synthase herbicide-tolerant mutant recorded fewest *Striga* attachments (Tuinstra et al. 2009). Introgression of major quantitative trait loci (QTLs) governing resistance to striga or major genes/transcription factor genes involved are identified, and genetic engineering approach is an effective way forward for their effective transfer and integration (Gressel 2010). Such resistance is difficult to overcome by the parasitic weeds and could be easily backcrossed into local varieties (Wang et al. 2009).

5.4.4 Morphological and Biochemical Markers in Disease and Insect Pest Resistance

Effective screening techniques and availability of biochemical, morphological or DNA markers associated or genetically linked to a specific disease or pest resistance, or at least to the specific component traits, would go a long way in sorghum breeding. Morphological and biochemical markers play a crucial role in the diagnosis and management of various biotic stresses in sorghum. Several phenolic compounds viz., allelochemicals like p-coumarates, p-hydroxybenzoates, flavanols and phytoalexins (3-deoxyanthocyanidins) have a key role in biotic stress resistance (Weir et al. 2004). Higher contents of proanthocyanidins, flavan-4-ols and 3-deoxyanthocyanidins (3-DAs) are involved in host plant resistance. 3-DAs are considered as better markers for resistance to biotic stresses as they associate with resistance to all biotic stresses (Dicko et al. 2005). The peroxidases (POXs) play a vital role against biotic and abiotic stress resistance by forming physical barriers through the synthesis of cell-wall polymers (lignin and suberin) (Cui et al. 1996).

5.4.4.1 Diseases

Antifungal proteins viz., chitinases, glucanases, sormatin and ribosome-inhibiting proteins play a significant role in imparting resistance to grain mold (Rodríguez-Herrera et al. 1999; Bueso et al. 2000). Further, traits like kernel hardness and pericarp color were found to be associated with grain mold resistance (Menkir et al. 1996). Traits such as kernel hardness with red pericarp, tan plant color kernels, high tannins along with a pigmented testa, as well as the pericarp intensifier (*I*) gene can enhance grain mold resistance (Esele 1995; Waniska et al. 2001). Involvement of peroxidases in fungal resistance was also inferred (Luthra et al. 1988).

5.4.4.2 Insect Pests

Insect/pest infestation in sorghum produces prussic acid or hydrocyanide (HCN), a toxic chemical which shows fatal response to herbivores. Two enzymes viz., glycosidase and hydroxynitrile lyases produce HCN from cyanogenic glycosides after mechanical stress or insect feeding (Freeman and Beattie 2008). Salicylic acid, jasmonic acid and abscisic acid, auxin and gibberellic acid are envisaged as defense responses to greenbug feeding (Park et al. 2006). Increased secondary metabolites also take part in shoot-fly resistance mechanism (Sharma et al. 2007). Biotic stress resistance in sorghum shoot-fly infestation is attributed in the form of tolerance, antixenosis (non-preference) and antibiosis which make them repellent to insects for feeding, shelter, egg laying and survival (Chamarthi et al. 2011; Mohammed et al. 2016). Biochemical factors like p-hydroxy benzaldehyde, luteolin, cinnamic acid and apigenin were connected with expression of shoot-fly resistance (Chamarthi et al. 2012). Further, polyphenol oxidase and peroxidase activities were upregulated in resistant genotypes which might have helped plants to tolerate infestation by shoot-fly (Padmaja et al. 2014). The pivotal role of total chlorophyll content, peroxidase and polyphenol activity in imparting resistance to shoot-fly was also noted (Singh et al. 2004b).

Shoot-fly resistance is associated with leaf glossiness and trichomes besides pigmentation and epicuticular wax (Dhillon et al. 2006; Kumar et al. 2014; Kiranmayee et al. 2015). The associated traits include reduced dead hearts incidence, improved leaf glossiness and reduced oviposition incidence (Anandan et al. 2009). Flies are reflected by the glossiness of leaves, larval movement on the surface of leaves is inhibited by dense trichomes, in turn acting as a physical barrier between the leaf and fly to prevent egg deposition (antixenosis). High seedling vigor leads to rapid growth of seedlings which hinder the larvae movement to the central leaf whorl thereby, reducing the frequency of dead hearts (Satish et al. 2009). Glumes of spikelets of gall midge resistant varieties are more tightly closed than those in susceptible varieties. A correlation between tannins and midge resistance was also noted (Santos and Carmo 1974; Sharma 1985, 1993). Spikelet morphology might be associated with antixenosis resistance mechanism (Henzell et al. 1994). A positive association between midge resistance and small glume size has been observed in sorghum (Jadhav and Jadhav 1978).

5.5 A Brief Account of Molecular Mapping of Resistance Genes and QTLs

Identification and mapping of major QTLs associated with disease resistance in sorghum pave way for the transfer of QTLs to varieties or parental lines to be used in breeding. Fine mapping of the QTLs would be revamped through the establishment of highly saturated genetic maps, restriction-site associated DNA

sequencing (RAD-seq) and single nucleotide polymorphisms (SNPs) (Zou et al. 2012). Six collinear independent component maps of sorghum were created and integrated into a single resource through the amalgamation of the component maps (Mace et al. 2009). A set of five genetic linkage maps based on RFLP markers were integrated to 10 linkage groups (Xu et al. 1994; Subudhi and Nguyen 2000). Thereafter, various research groups saturated the linkage maps with amplified fragment length polymorphism (AFLP) markers (Ramu et al. 2009). Over 323 RFLPs and 143 simple sequence repeats (SSRs) were utilized for the construction of high-density linkage map (Bhatramakki et al. 2000; Bowers et al. 2003). Later, AFLPs, SSRs and RFLPs markers constituting 2926 markers were further used to saturate the former map (Menz et al. 2002). EST-SSRs and candidate genes-based SSR markers have been used in constructing linkage maps (Ramu et al. 2009; Reddy et al. 2012; Zou et al. 2012).

5.5.1 Mapping Populations

Different research groups across the globe have developed specific bi-parental mapping populations that have paved the way for the identification and mapping of QTLs associated with resistance to several pests and diseases in sorghum. In general cross between two, sometimes more parents are involved in obtaining mapping populations. The parents selected and the mating design for the development of the mapping populations largely depend on the purpose of the study. F_2 , F_2 -derived F_3 ($F_2:F_3$), recombinant inbred lines (RILs), backcross inbred lines (BILs), near-isogenic lines (NILs), doubled haploids (DHs), multi-parent advanced generation intercross (MAGIC), chromosomal segment substitution lines (CSSLs), nested association mapping (NAM) population etc. are the several types of mapping populations being used for QTL mapping (Singh and Singh 2015). For biotic stress resistance BILs, RILs and populations derived from multi-parental lines such as MAGIC and NAMs are more specifically used (Arrones et al. 2020). Identification and mapping of important QTLs for pest and disease resistance in sorghum has enhanced with the use of genomic tools and mapping populations.

5.5.2 QTLs Mapped Using Different Mapping Populations

5.5.2.1 QTLs Associated with Diseases

The SNP markers linked to rust resistance have been identified and studied in detail (Upadhyaya et al. 2013b). The GWAS approach elucidated over 64 significant QTLs for rust including the earlier reported ones (Tao et al. 1998; Mohan et al. 2010; Upadhyaya et al. 2013b). Besides, a major QTL of the genome SC414-12E on chromosome 5 explained 20–39% of PVE in four environments (Kimball et al.

2019). Anthracnose resistance gene was identified by a closely linked RAPD marker *OPJ OI₁₄₃₇* through bulk segregant analysis of derived RILs. QTLs for anthracnose on chromosome 9 found to be consistent across all the environments tested. The genomic regions reported earlier by Tao et al. (1998) and Klein et al. (2001) for rust and grain mold resistance, were found relevant to ergot disease resistance. Further, the presence of additive and non-additive gene actions for charcoal rot resistance has been noticed (Rao et al. 1993). Three traits, number of internodes crossed by the rot, crop lodging and length of infection conferred genetic basis to charcoal rot (Reddy et al. 2008). Haussmann et al. (2004) revealed five QTLs related to striga resistance in two RIL and were common across two mapping populations.

5.5.2.2 QTLs Associated with Insect Pests

Four major QTLs on chromosome 9 from PI 607900 resistant to greenbug biotype I were identified. Two major QTLs—*sbi09ii* and *sbi09iii* described up to 39.8 and 34.7 per cent variability for greenbug infestation (Punnuri et al. 2013). Three QTLs located on LG-A, LG-G and LG-J, respectively, explained 8.8%, 15% and 33.9%, phenotypic variation for gall midge resistance (Tao et al. 2003). Some shoot fly resistance (SFR) sources identified after evaluating the marker traits in sorghum germplasm have been exploited in breeding programs (Chamarthi et al. 2011; Kumar et al. 2014). Using crosses 296B (susceptible) × IS18551 (resistant) (Satish et al. 2012b) and cross 27B (susceptible) × IS2122 (resistant), SFR QTLs were mapped (Aruna et al. 2011). Four SFR QTLs were introgressed and the progenies harboring different combinations of major QTLs showed resistance which was evidenced by the fewer number of shoot flies (Abinaya et al. 2019). A set of 19 putative QTLs associated with resistance to shoot-fly including *qDH9.1* (dead heart) and *qEC9.1* (oviposition) explaining 15.03 and 18.89% phenotypic variance have been reported (Vikal et al. 2020). The genes producing allelochemicals, receptor kinases, and ubiquitin-proteasome degradation in the pathways as well as the candidate genes, like *cysteine protease* and cytochrome P450 were identified within the predicted QTL regions (Vikal et al. 2020).

5.6 Marker-Assisted Breeding for Biotic Stress Management in Sorghum

With the availability of large-scale sorghum genomic resources and use of DNA markers, breeding for desired agronomic traits and biotic stress resistance is becoming increasingly relevant. Affordable high-throughput genotyping coupled with throughput genome sequencing is rendering the use of molecular markers in germplasm diversity assessment, QTL mapping facilitating MAS. Resistance to

major pests and diseases is governed by multiple genes, which are seldom amenable to achieve an appreciable increase in resistance due to their strong influence by the environment (Tao et al. 2003; Mohammed et al. 2016). The molecular breeding approaches have been deployed in many crop species including sorghum to achieve delivery of results quickly with much greater precision (Kiranmayee et al. 2015).

5.6.1 *Germplasm Characterization*

Genetic resources as classified based on morphological characteristics, divided *Sorghum bicolor* into five major races: *bicolor*, *guinea*, *caudatum*, *kafir*, and *durra* and over ten possible hybrid groups (Harlan and de Wet 1972; Harlan and Stemler 1976; De Wet 1978). There are several ‘wild’ species and sub-species within *S. bicolor* and races within each subspecies (Snowden 1955). Sorghum has over 3475 accessions with over 242 mini core collection that include all five races and representation of geographic regions (Prasada Rao and Ramanatha Rao 1995; Upadhyaya et al. 2009; Dahlberg et al. 2012). Association mapping in mini-core collection for grain mold resistance using 14,739 SNP markers led to the identification of two linked marker to rust resistance (Upadhyaya et al. 2013b). Over 3367 accessions involving cultivated and wild relatives were genotyped using 41 SSR markers in which 78.3% of the SSR alleles were detected with a mean of 14.9 alleles per marker, comparable to the original allelic richness (Billot et al. 2013). Further, in an another attempt, a genome-wide association analysis using 268,289 SNPs, two loci linked to low seed deterioration and seedling emergence rate was identified (Cuevas et al. 2019).

5.6.2 *Marker-Assisted Gene Introgression*

Both the efficiency and precision of crop breeding can be achieved with the use of DNA markers. Molecular mapping of major QTLs for disease and pest resistance has facilitated the transfer of QTLs to the agronomically superior varieties in the shortest possible time using MAS strategies (Dormatey et al. 2020). Marker-assisted gene pyramiding (MAGP) can pyramid disease/pest resistance genes into single cultivar (Sanchez et al. 2000). Marker-assisted recurrent selection (MARS) is a strategy to accumulate favorable alleles i.e., multiple QTLs controlling resistance through genotypic selection and inter-crossing in repeated cycles of selection resulting in enhanced efficiency of recurrent selection and accelerated breeding (Ribaut et al. 2010; Dormatey et al. 2020). The process of stacking of genes/QTLs into a single elite cultivar background can now be efficiently performed using backcrossing or pedigree approaches with molecular markers thus eliminating the elaborate and costly process other ways (Kole 2006). Pyramiding of multiple genes/QTLs can lead to improved resistance (Werner et al. 2005).

Molecular breeding tools enable tracking the introgression of several *R*-genes from various sources into a single cultivar (Witcombe and Hash 2000). Three breeding strategies viz., stepwise transfer, simultaneous/synchronized, and convergent backcrossing are being employed for marker-assisted gene pyramiding (MAGP). MAS is needed to select pyramided resistance genes in the segregating progeny generation (Werner et al. 2005).

As many as five putative SFR QTLs for the component traits from IS18551 were introgressed through marker assisted back-cross breeding (MABCB) (Mehtre 2006; Jyothi et al. 2010). SFR QTLs were introgressed into 296B backgrounds and introgression lines (ILs) from 296B × IS18551 and BTx623 × IS18551 (Deshpande et al. 2010; Jyothi et al. 2010; Satish et al. 2012a) were field evaluated for the traits (Reddy et al. 2012). A total 136 BC₃ and 30 BC₄ plant progenies from crosses BC₂ X AKSV 13 R and BC3 X AKSV 13 R, respectively, were screened for the recovery of donor alleles in the elite background (Wagh et al. 2016). In addition, three QTLs associated with shoot-fly resistance were also introgressed into an elite cultivar ICSB 29004 and Parbhani Moti, all the derived introgression lines had higher shoot-fly resistance levels (Gorthy et al. 2017).

A gene associated with leaf blight resistance from G-118 was introgressed into the susceptible cultivar HC-136, using linked DNA marker (Mittal and Boora 2005). RILs with both resistant and susceptible reaction were screened individually with marker *Xtxp 309*, which produced amplification in 23 of the 26 resistant RILs, but no amplification in 25 susceptible RILs. This indicated the potential application of this marker in MAS for gene introgression (Mittal and Boora 2005). Further, eight putative QTLs were detected for resistance to sorghum downy mildew in a set of 50 inbred lines derived from the cross CML153 (susceptible) X CML226 (resistant) using 128 SSRs and 191 SNPs, introgression effort developed 33 resistant lines (Nagabhushan 2014). In a separate effort of using DNA markers for striga resistance, markers spanning through the QTLs conferring resistance to striga parasite were identified and the same markers were used in introgression to make headway towards developing resistant lines (Hausmann et al. 2004; Satish et al. 2012a; Mohamed et al. 2014; Yohannes et al. 2015). The QTLs of striga resistance in N13 were transferred to a farmer-preferred sorghum variety through MABCB using flanking SSR markers (Yohannes et al. 2016; Afolayan et al. 2019).

5.6.3 *Limitations and Prospects of MAS and MABCB*

MAS and MABCB approaches, even though adopted to breed resistance against biotic stresses, the complex quantitative traits have recorded marginal success as the QTLs for such traits partially explain the phenotype. The impact and application of MAS in plant breeding are still below the hypothetical possibilities. This could be attributed majorly due to the difficulty in identifying major QTLs with an adequate stable effect across environments and genetic backgrounds. The limited number of polymorphic markers in the breeding material and diverse mapping populations is

difficult to compare, assessment of QTL x environment interaction effect pose a complicate interpretation (Collard and Mackill 2008; Ribaut et al. 2010; Delannay et al. 2012). Further, genomic selection is a hope to solve this problem, where unmapped QTLs of small individual effects selected together by the plant breeders (Tuberosa 2012; Sakiyama et al. 2014). High throughput genotyping, phenotyping and more automatic ways would enhance the use of MAS in plant breeding (Gorthy et al. 2017).

5.7 Brief on Genetic Engineering for Resistance Traits

Conventional plant breeding methods used to develop cultivars resistant to multiple pests and diseases in sorghum are inadequate when the desirable genes are limited in the gene pool of cross-compatible species or when such genes restricted linkage-drag (Crews and Cattani 2018). Genetic transformation and genome editing enable incorporation of beneficial genes across genera into sorghum with limited genetic diversity in the desired traits (Liu et al. 2014). Insect pests with wide host range, evolving races of pathogens and low level of resistance in the cultivated sorghum germplasm have made molecular plant breeding approaches as highly desirable (Madhusudhana 2015). Insecticidal crystal proteins (CRY) from *Bacillus thuringiensis* (*Bt*) are very effective against the lepidopterans and dipterans. *Bt* and other genes including protease inhibitors, enzymes, secondary plant metabolites and plant lectins are being evaluated to reduce losses due to insect pests (Sharma et al. 2004; Visarada and Kishore 2007). Progress in sorghum transformation has been hindered by the challenges associated with recalcitrance to genetic transformation (Jeoung et al. 2002; Girijashankar et al. 2007). Different gene transfer methods are being used in sorghum so far, which include, *Agrobacterium*-mediated indirect gene transfer; electroporation and particle bombardment (Ahmed et al. 2018). *Agrobacterium*-mediated transformation is simple and precise in the integration of the transgene. However, monocotyledons such as sorghum are less responsive to *agrobacterium* infection. *PR* genes for *fusarium stalk rot* disease resistance were introduced into sorghum genotypes through *Agrobacterium*-mediated gene transfer. Despite the basic research, sorghum is still one of the most recalcitrant crops to transformation and regeneration (Raghuwanshi and Birch 2010).

5.7.1 Transgenic Resistance to Fungal Diseases

Sorghum is highly vulnerable to multiple fungal diseases causing decreased grain quality and yield loss. Genes encoding fungal cell wall hydrolyzing enzymes such as glucanases, chitinases and chitosanases are potential transgene candidates for developing fungal disease resistance in sorghum (Muthukrishnan et al. 2001). Chitinases and chitosanases degrade the components of fungal cell walls i.e., chitin

and chitosan and lyse the fungi. The first fungal resistance gene -*rice chitinase* (*G11*) was introduced into the sorghum inbred 'Tx430' along with *bar* gene and a plasmid DNA into the calli of immature zygotic embryos (Zhu et al. 1998). Thaumatin-like proteins (TLPs) are one more class of pathogenesis-related (PR) proteins that have shown antifungal activity and have been used as transgenes for enhancing fungal resistance (Mahdavi et al. 2012). Two PR genes viz., *rice chitinase* (*G11*) and *tlp* (Thaumatin-like protein) were introduced into three different sorghum inbred lines (Jeoung et al. 2002). Chitinase gene, *OschIII* fused with CaMV 35S promoter prospected for stalk rot resistance (Muthukrishnan et al. 2001). Transformation of sorghum with *tlp* gene along with green fluorescent protein (*gfp*) under the maize *ubi1* promoter exhibited enhanced resistance to fungal diseases. Expression of *gfp* was highly correlated with the expression of *tlp*, which was further confirmed by western blot analysis (Gao et al. 2005a). *In planta* and *ex planta* anthracnose infection assays revealed transgenic line KOSA-1 to be more resistant to anthracnose in comparison to its non-transgenic wild type AT412 (Ayoo 2008; Anami et al. 2016).

5.7.2 Transgenic Resistance to Insect Pests

Insecticidal crystal proteins are potential candidates for insect resistance in many crop plants (Roh et al. 2007; Jain et al. 2016). Many *Bt* toxin genes have been transferred into sorghum to attain resistance against insect pests. Stem borer is an important pest in sorghum. Sorghum genotype BT × 623 was transformed with the *cryIAc* gene under the control of a wound-inducible promoter from the maize protease inhibitor gene (*mpiC1*) via particle bombardment of shoot apices. Transgenic lines showed up to 60% reduction in leaf damage, 40% larval mortality and 36% weight loss in the survived larvae of stem borer. However, *Bt* protein accumulation under the inducible promoter was very low at 1–8 ng/g of fresh tissue, which led to partial resistance (Girijashankar et al. 2005). Sorghum varieties 115, ICS21B and 5–27 were transformed with the *cryIAb* gene and the transgenic lines showed high resistance levels to pink rice borer (Liu et al. 2015). Sweet sorghum varieties 'BABUSH' and 'MN-3025' transformed with *cryIAh* using *Agrobacterium*-mediated transformation have shown high insect-resistance to Asian corn borer (*Ostrinia furnacalis*) (Zhao et al. 2011). Enhanced accumulation of the *Bt* protein in leaves by 30 to 50-fold (35–500 ng/g fresh leaf) by expression of *cryIAa* and *cryIB* genes under the influence of maize *ubiquitin-1* promoter was reported during the susceptible plant growth period. Leaf consumption by the stem borer in the transgenic sorghum leaves was significantly lower (20–30%) compared to their feeding on non-transgenic lines (77–80%). Transgenic lines also showed a significant reduction in the leaf damage (55–78%) over their non-transgenic controls. Where, the larval mortality was appreciably high (60–90%) in transgenic lines as compared to (14–24%) non-transgenic control (Visarada et al. 2014). Higher expression of *Bt* protein is crucial for achieving superior insect control, which may

be achieved by placing the *Bt* genes under suitable promoters such as maize ubiquitin.

Transgenic glyphosate-resistant crops overexpressing 5-enolpyruvylshikimate-3-phosphate synthase (*cp4 epsps*) gene accelerated widespread use of glyphosate (Duke and Powles 2008) in controlling recalcitrant weeds such as Johnsongrass. RNAi is one of the most successful strategy in target trait improvement apart from its role in identifying gene function by silencing different pathogens/pests as well as plant genes (Stach and Good 2011; Banerjee et al. 2017; Majumdar et al. 2017; Zhang et al. 2017a). Virus-induced gene silencing (VIGS) efficiency in sorghum was significantly enhanced with an antisense strand of a gene in *Brome mosaic virus* (BMV) (Singh et al. 2018) (Table 5.1).

5.8 Brief Account on Bioinformatics as a Tool for Biotic Stress Resistance Breeding

Advances in disciplines that are contributing to the generation of genomic resources and data analytics have made a significant impact for structural and functional genomics of sorghum in the past decade. The next-generation sequencing platforms have greatly facilitated advanced assessment of sorghum genome, variety of transcriptome profiling attempts with deep insights into the structural organization of the genome; gene prediction; gene annotation and response of genes in variable biotic and abiotic conditions. The developed bioinformatics tools assist in filtering of data sets of various types, the correct interpretation of specific outcomes of *in silico* analytics of the data and its targeted views to elucidate the candidate gene sets that have potential applications in the breeding of sorghum for various biotic stress resistances (López de Maturana et al. 2019). The use of publicly available genomic data sets has helped the researchers to annotate key genes for their target traits in sorghum. Since the genome of sorghum is sequenced and high throughput datasets are publicly available, the bioinformatics pipelines can effectively identify putative candidate genes for various biotic stress responses. These potential candidate genes would be useful to develop the markers for the genotyping of breeding populations for the identification of a superior lines (de Oliveira et al. 2018). Databases in sorghum include; **SorGSD**: Web-portal with a comprehensive database of genomic variation across all types of cultivated and wild sorghums (Luo et al. 2016) and **SorghumFDB** covering transcription factors, regulators, protein kinases, ubiquitin, monolignol biosynthesis-related enzymes, carbohydrate-active enzymes, cytochrome P450, organelle-genes and R-genes. It acts as a genome browser for comprehensive coverage of gene annotations, miRNA information, gene loci conversions, orthologues in model plants like arabidopsis, maize and rice (Tian et al. 2016).

Through genomics, identified genomic regions could be incorporated to impart resistance to sorghum midge (Yazawa et al. 2013). Transcriptomic analysis of Cv.

Table 5.1 Transgenes conferring insect and disease resistance in sorghum

Transgene	Source	Target organism	Transformation method	Reference
<i>Insect resistance</i>				
<i>CryIAc</i>	<i>Bacillus thuringiensis</i>	Stem borer	Biolistic	Girijashankar et al. (2005)
<i>cryIAb</i>	<i>Bacillus thuringiensis</i>	Pink rice borer	Agrobacterium	Liu et al. (2015)
<i>cryIAh</i>	<i>Bacillus thuringiensis</i>	Asian corn borer	Agrobacterium	Zhao et al. (2011)
<i>cryIAa</i> and <i>cryIB</i>	<i>Bacillus thuringiensis</i>	Stem borer	Biolistic and Agrobacterium	Visarada et al. (2014)
<i>Disease resistance</i>				
chitinase (<i>GI1</i>)	<i>Oryza sativa</i>	Fungi	Biolistic	Zhu et al. (1998)
chitinase (<i>chII</i>)	<i>Oryza sativa</i>	<i>Fusarium thapsinum</i>	Biolistic	Muthukrishnan et al. (2001)
chitinase	<i>Oryza sativa</i>	Fungi	Agrobacterium	Arulsevi et al. (2010)
chitinase (<i>HarChit</i>)	<i>Trichoderma harzianum</i>	<i>Colletotrichum sublineolum</i>	Biolistic	Ayoo (2008)
chitosanase (<i>HarCho</i>)	<i>Trichoderma harzianum</i>	<i>Colletotrichum sublineolum</i>	Biolistic	Ayoo (2008)
Thaumatin-like protein	–	Fungi	Agrobacterium	Gao et al. (2005b)

SIL-05 and *Bipolaris sorghicola* led to the identification of genes in host-pathogen interaction (Mizuno et al. 2012). The genes encoding hyphae related proteins and enzymes involved in plant cell wall degradation elucidated from pathogen transcriptome data sets besides genes encoding WRKY, receptors of LLR domain and class III peroxidase are relevant for functional genomics analysis in sorghum (Yazawa et al. 2013). Molecular interpretation of charcoal rot defense mechanism was unraveled by expression profiling of genes in resistant and susceptible cultivars (Sharma et al. 2014b). A major QTL on linkage group 5 in the cross of BTx623/SC748-5 for anthracnose resistance analyzed by sequencing genomic DNA of SC748-5 and compared to BTx623 genome sequence (Burrell et al. 2015; Poloni and Schirawski 2016). Transcriptional changes and network analysis were decoded in a resistant and a susceptible genotype of sorghum to sugarcane aphids. A suite of abundantly expressed genes were recovered across genotypes and nucleotide-binding-site-leucine-rich repeat (NBS-LRR) and disease resistance genes were recognized (Kiani and Szczepaniec 2018; Tetreault et al. 2019). Correlation-based network analyses vis-a-vis metabolic pathway analysis revealed that multi-component defense response characterized by a functional defense-related molecular cues are involved in pathogen invasion (Tugizimana et al. 2019). Metabolomics of white sorghum-isolated *Burkholderia andropogonis* interaction revealed the alterations in the levels of phytohormones that marked the onset of defense in sorghum (Mareya et al. 2019, 2020).

5.9 Recent Concepts and Strategies Developed

5.9.1 Genome Editing

A multitude of pathogens and insect pests comprising viruses, bacteria, fungi, insects and even parasitic plants affect sorghum globally with significant yield losses which in turn influence the food supply (Mushtaq et al. 2019; Yin and Qiu 2019). The strategy to control various diseases and pests involve widespread use of hazardous pesticides, which can be directly or indirectly deleterious to nature (Tyagi et al. 2020). Developing disease and insect pest resistant crops through various breeding approaches are sustainable and ecofriendly. In addition to the conventional transgenic approach, recent genome editing for biotic stress has greater potential in breeding programs. The biotic stress resistance being complex in nature is governed by several genes each with small effect. Some of these key genes could be potentially edited to create new alleles that can produce a larger desirable effect, thus re-orienting the process of breeding. More recently, genome editing technologies have emerged and evolved to enable rapid and precise manipulation of specific DNA sequences for developing biotic stress-resistant germplasm (Shi et al. 2017; Gao 2018; Yin et al. 2018). Genome editing involves engineered nucleases containing a non-specific nuclease domain fused with a

sequence-specific DNA binding domain, which can cleave the targeted gene precisely that can be repaired through specific genetics approaches. Zinc finger nucleases (ZFN), the first-generation editing technology are the chimeric proteins that consist of FokI cleavage domain and non-specific DNA cleavage domain (Fiaz et al. 2019; Ansari et al. 2020). Transcription activator-like effectors nucleases (TALENs) discovered in *Xanthomonas* consists of the amino acid repeats in the central DNA binding domain that recognizes one nucleotide in the target sequence. The repeat variable di-residue (RVD) which is located at 12 and 13 positions determines the specificity of TALEN. Once TALEN_S are translocated to the nucleus, they bind to the target DNA strand in an opposite orientation. The FokI gets dimerized and cleaves at the spacer region resulting in double-strand breaks (DSB) in the target region (Jaganathan et al. 2018; Li et al. 2018). CRISPR/Cas System: clustered regularly interspaced short palindromic repeats (CRISPR), is a prokaryotic system observed for the first time in *Escherichia coli* that contains short repeated sequences separated by spacers with unique sequences (Ishino et al. 1987; Rath et al. 2015). A large recognition (REC) lobe determines the Cas9-specific function, whereas the small nuclease (NUC) incorporates two nuclease domains, RuvC and HNH, and a proto-spacer adjacent motif (PAM)-interacting domain (PI). The Cas9/single guide RNA (Cas9-sgRNA) complex probes a DNA sequence for rigorous protospacer adjacent motif (PAMs) using the Watson–Crick pairing principle (Song et al. 2016).

5.9.1.1 Genome Editing in Sorghum

The type II CRISPR/Cas, Cas9-sgRNA system was employed in sorghum as well as in arabidopsis and tobacco. *Agrobacterium tumefaciens* mediated method for green fluorescent protein-coding gene transfer was used and mutagenic effects of the Cas9/sgrRNA system in immature sorghum embryos were observed (Jiang et al. 2013). CRISPR/Cas9 system has been investigated by targeted editing of cinnamyl alcohol dehydrogenase (CAD) and phytoene desaturase. Genotype TX430 was edited successfully with effective biolistic bombardment (Li et al. 2018). CRISPR/Cas9 approach was applied to edit the *chlorophyll-a oxidase* (CAO) gene in sorghum protoplasts (Meng et al. 2020). Fourteen protoplasts showed precise editing in target gene region which could be a possible model for precise editing study in sorghum for improvement concerning agronomically important traits. Although, till date, there is no study reported concerning the use of genome editing for biotic stress resistance in sorghum, the use of the conventional transgenic approach for improving resistance is reported by a number of studies. Transformation of sorghum with *rice chitinase* for resistance against stalk rot, expression of the *cryIAC* gene against sorghum spotted stem borer, *chitinase* & *chitosanase* genes against anthracnose, expression of Bt *cryIAh* gene (Zhu et al. 1998; Muthukrishnan et al. 2001; Girijashankar et al. 2005; Akosambo-Ayoo et al. 2011; Liu and Godwin 2012) envisages that the model transgenic studies in sorghum will pave the path for precise breeding and may facilitate the development of product germplasm governing biotic resistance through the editing of same genes.

5.9.2 Nanotechnology

Nanotechnology is currently being explored for agricultural applications, including, finding solutions for yield loss due to insect pests and diseases (Balaure et al. 2017; Sinha et al. 2017). Current pest management relies on the use of chemicals with all their side effects and environmental concern (Ghormade et al. 2011; Worrall et al. 2018). The nanoparticles, besides other ways, aid enhanced solubility of pesticides, increased shelf life and these protect plants from target pest (Hayles et al. 2017). Nanoparticles of Ag, Cu and Zn could be utilized as a potential method for suppressing diseases in crop plants (Elmer and White 2018; Malandrakis et al. 2019; Vanti et al. 2019). The application of nanotechnology with the use of emerged nanomaterials may heighten the sustainable productivity through effective insect pest and disease management (Giannousi et al. 2013; Imada et al. 2016).

5.10 Conclusion and Future Perspectives

Sorghum being an important cereal crop for low endowed and climatically challenging situations of the world, to achieve the sustainability for food and fodder in such regions, the development of biotic stress-resistant cultivars coupled with drought stress tolerance is crucial. As such, yield stability and grain quality are severely affected by various biotic stresses including insect pests, diseases and parasitic weeds, which hamper this crop at all stages including storage. Biotic stresses pose daunting challenges to the realization of its yield potential, and development of resistant cultivars through host plant resistance is most opted, as a great deal of germplasm diversity exists and serves as a source of resistant genes. However, on practical scale, attempts to increase the production of sorghum with the introduction of new high yielding varieties and hybrids have been largely unsuccessful because of their susceptibility to various biotic stresses (Kishore 2001; Kiranmayee et al. 2015). The limited number of resistant accessions and their overall phenotype may constrain the development of new varieties. The wide host range for many of the insect pests and low level of resistance in the cultivated germplasm necessitates the use of wild relatives and new parental lines having the potential genes for various biotic stress resistance to mitigate the negative effect. Advent of molecular tools has great scope in accelerating the process of breeding, and in turn resulting the enhanced resistance in the form of horizontal as well as vertical resistance. Besides, the conventional process of breeding is highly labour-intensive and time-consuming (Sharma et al. 2005) and the resistance being highly complex, it is essential to deploy molecular markers linked to QTLs or any gene and these QTLs/genes are to be introgressed to increase the efficiency of conventional breeding (Kumar et al. 2014; Kiranmayee et al. 2015).

Fine mapping of the mapped QTL regions and significant marker trait associations through GWAS is needed. Further validation of QTLs provides great promise

for employing MAS in sorghum improvement. Genes responsible for resistance such as leaf blade glossiness and trichome density and other associated genomic regions need to be cloned and their introgression and expression level studies should be made to enhance the resistance related genetic architecture. Combinatorial approaches with conventional plant resistance along with novel genes such as *Bt* gene for increased resistance is highly desirable. An integrated synergistic system involving plant breeding and genomics research using advanced molecular tools such as high-throughput sequencing and large-scale genotyping technologies followed with MAS is a way forward to improve sorghum biotic stress resistance. Advances in new genomic tools such as genome sequencing, DNA microarrays, RNA-sequencing, real-time PCR, protein expression profiling, metabolomics strategies and bioinformatics allow more in-depth knowledge about the genetics of host defense and host-plant resistance mechanisms to biotic stresses (Kumar et al. 2014). In addition, sequencing of sorghum whole genome and its availability on publically available data sets of genomic resources of various types is expected to accelerate for rapid trait discovery and introgression (McCormick et al. 2018).

Transcription factors are candidates of choice to alter the agronomically relevant traits and to boost the resistance to biotic stresses and several transcription factors families, such as WRKY, NAC, MYB, DREB, and bZIP, in response to biotic stresses have been identified and characterized in sorghum. As such transcription factor responses to biotic stresses are highly complex with larger effects and complex cross-talk between different signal transduction pathways (Baillo et al. 2019). The findings from previous reports indicate the potential application of TF genes to enhance stress resistance in important crops, however, extensive studies for understanding the mechanisms of these TFs are required. Studies involving combinatorial approaches of TFs and small RNAs are expected to unravel the pathways and key genes for biotic stress resistance, such genes will be of key in utilizing the upcoming opportunities such as genome editing and genomics assisted breeding. The availability of complete genome sequences in sorghum and breakthroughs in sequencing technology have facilitated the identification and characterization of TFs (McCormick et al. 2018).

In future, it is crucial to pyramid multiple genes to achieve multiple resistant varieties through MABCB. So far, no QTL has been found to regulate multiple pest/disease resistance in sorghum (Romana et al. 2018). Hence, future research efforts should focus on identifying genetic loci responsible for multiple disease resistance, new sources of resistance, characterization of resistance genes, and dissecting the network of resistance gene regulation (Dormatey et al. 2020). Genomic selection has great promise in exploiting unmapped QTLs of small individual effects at the whole plant level which could be deployed in plant breeding endeavors, this approach expected to be relevant in sorghum as it has great genetic diversity (Yano and Tuberosa 2009). The newly developed genomic approaches would rapidly accelerate applications to many different research areas ranging from marker discovery; genetic diversity; and linkage/association mapping

to the genomic selection, physical mapping, gene discovery and genomic-assisted breeding to improve biotic stress resistance in sorghum.

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