Chapter 7
Genomic Designing for Climate Smart Finger Millet

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Abstract Finger millet is a nutritious cereal crop mainly grown in eastern Africa and southern parts of India. The crop has an incredible ability to adapt to adverse agro-ecological conditions, and is therefore a favorite of smallholder farmers in the tropics, especially women. Finger millet grain is gluten free and exceptionally rich in micronutrients including calcium, folic acid and iron. Despite its unique quality, there has been limited research investment in finger millet resulting in the lack of genetic and genomic resources for more efficient breeding. The abundant genetic resources at the center of origin are yet to be fully exploited for crop improvement, and to date, very few pre-breeding programs exist. Several studies indicate the potential use of the secondary and tertiary gene pools to broaden the narrow genetic base that has been created by the inbreeding nature of the crop. The recent

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availability of draft whole genome sequences and a robust genetic linkage map, now make it possible to implement large-scale genomics-assisted breeding in finger millet. Comparative mapping with closely related and well-studied crops such as rice, provide an opportunity to understand the complex tetraploid genome more efficiently. With the increasing health awareness, and the growing middle class in Africa and Asia, there is likely to be a higher demand for the nutritious finger millet. Breeders will need to generate relevant populations and increase the yield of finger millet to its full potential in order to meet the demand. The current investment in the generation of genomic resources will need to be matched with investment in phenotyping and germplasm characterization to enable more efficient breeding in finger millet. We discuss the genetic and genomic resources available for finger millet and how they can be exploited to enhance its adaptability to climate change.

Keywords *Eleusine coracana* · Climate change · *Striga* · Blast disease · Tetraploid

7.1 Introduction

Small millets, the earliest domesticated crop species of the world, are a heterogeneous group of cereals that includes finger millet (*Eleusine* spp.), foxtail millet (*Setaria italica*), pearl millet (*Pennisetum glaucum*), little millet (*Panicum miliare*), proso millet (*Panicum miliaceum*), kodo millet (*Paspalum scrobiculatum*), barnyard millet (*Echinochloa colosna*), fonio (*Digitaria exilis*), and teff (*Eragrostis tef*) (Seetharam et al. 1986). They are often grown under harsh environments by small-scale farmers. They are nutritionally rich, genetically diverse and are recognized as crops for new green revolution (Goron and Raizada 2015). Millets are increasingly playing an important role in marginal environments, which are especially vulnerable to climate variability and longer-term climate change scenarios such as increased temperatures and unpredictable rainfall (Padulosi et al. 2009). Finger millet is widely cultivated in the tropical and subtropical regions of Africa and India and ranked third in importance among millets after pearl millet (*Pennisetum glaucum*) and foxtail millet (*Setaria italica*) (Reddy et al. 2009). It is also the most important millet in eastern Africa.

The exact origin of finger millet has been a subject of debate with different authors reporting different locations within eastern Africa. Vavilov (1951) considered finger millet an indigenous crop to Ethiopia and the high plateaus of Abyssinia while Purseglove (1972) reported Uganda as the center of origin. Kenneth and LeRoy (1977) reported the eastern Sudan zone and the highlands stretching from Ethiopia to Uganda as a possible area of domestication of this crop. Biosystematics, ethno-botanical, genetic and linguistic evidence confirmed that the East African highlands, particularly Uganda and Ethiopia, are a possible center of origin for finger millet (Hilu and De Wet 1976). Archaeological record provides evidence for the oldest domesticated finger millet at a prehistoric site in

Axum, Ethiopia, dating back some 5000 years (Hilu et al. 1979). Moreover, vast genetic diversity exists within Ethiopia and Uganda providing further proof that this region is the primary center of origin. From east Africa, the crop was introduced to India over 3000 years ago (Hilu et al. 1979; National Research Council 1996), where it is now an important staple food.

Finger millet belongs to the genus *Eleusine* Gaertn, family Poaceae, subfamily Chloridoideae. The genus comprises eight species including *E. coracana, E. kigeziensis*, *E. indica*, *E. intermedia*, *E. floccifolia, E. tristachya, E. jaegeri* and *E. multiflora. E. coracana* is comprised of two subspecies; *E. coracana* subsp. *coracana,* which is the cultivated finger millet; and *E. coracana* subsp. *africana*, its wild progenitor (Dida et al. 2007). The genus is characterized by three different basic chromosome numbers of $x = 8$, 9 or 10. Dida and Devos (2006) suggested the categorization of the genus *Eleusine* into an *AA* genome group comprising *E. indica* and *E. tristachya* and a *BB* genome group comprising three species namely *E. floccifolia*, *E. intermedia* and *E. multiflora* with tetraploids (*E. coracana* and *E. kigeziensis*) having a combination of AABB. Recent reports (Dwivedi et al. 2012; Vetriventhan et al. 2016) suggest categorization into four genome groups; AA (*E. tristachya* and *E. indica*), BB (*E. floccifolia*), CC (*E. multiflora*) and DD (*E. jaegeri*), with *E. intermedia* being a mixture (AB) and the tetraploids having AABB (*E. coracana*) and AADD (*E. kigeziensis*).

E. intermedia, E. indica, E. floccifolia, and *E. tristachya* are diploids with $2n = 2x = 18$. *E. multiflora* is a diploid with $2n = 2x = 16$ while *E. jaegeri* is a diploid with $2x = 2n = 20$ (Devarumath et al. 2005). *Eleusine coracana* and *E. kigeziensis* are tetraploids with $2n = 4x = 36$. *E. indica* (AA) is believed to be the AA genome donor for *E. coracana* (AABB) while the BB genome donor remains unknown. *Eleusine coracana* subsp. *coracana* is the only cultivated crop of the genus *Eleusine* and has four cultivated races, namely, *elongata, plana, compacta,* and *vulgaris* (Upadhyaya et al. 2010). *Eleusine coracana* subsp. *africana* has two wild races; *africana* and *spontanea* (Upadhyaya et al. 2010). *Eleusine indica* (goosegrass) is categorized as one of the most problematic weeds in the world (Holm et al. 1977; Devarumath et al. 2005).

The cultivated finger millet (*Eleusine coracana* supsp. *coracana*) is a food staple of millions smallholder farmers (Babu et al. 2007; Kumar et al. 2016) and occupies about 12% of the global small millet area, across arid to semi-arid tropics of Asia and Africa (Mirza et al. 2015). It represents one of the critical plant genetic resources for the agriculture and food security of farmers inhabiting arid, infertile and marginal lands (Barbeau and Hilu 1993). India is the largest producer of finger millet in Asia, while in Africa the largest producing region extends from the Rift Valley, Nyanza and Western provinces of Kenya into Uganda. In India, it is cultivated mainly in the terai regions of Himalayas and in the southern peninsula (Bhatt et al. 2011). Other producers of finger millet include Tanzania, Ethiopia, Rwanda, Zaire, Zambia, Zimbabwe, Eritrea and Somalia in Africa, while China, Myanmar (Ekwamu 1991), Nepal, and to some extent, Bhutan and Sri Lanka are the other producers in Asia.

7.2 Prioritizing Climate Smart Traits

Among the merits of finger millet is its ability to adapt to adverse agro-ecological conditions such as soil acidity, moisture stress, minimal inputs and marginal land where other crops cannot perform well (Upadhyaya et al. 2007). Finger millet plants have the advantage of assimilating carbon dioxide through the C4 photosynthetic pathway resulting in more efficient photosynthesis, and therefore more efficient use of water and nutrients. The crop is mainly grown by subsistence farmers in semi-arid areas where it is known to save the lives of poor farmers from starvation during extreme drought (Kotschi 2006). However, despite finger millet's incredible ability to withstand drought, FAO (2005) reports that the anticipated climate change may pose a negative impact on food production and food security, especially in drought-prone regions, where finger millet is mainly grown. Besides, pests and diseases are most likely to be influenced by the changing temperatures (Stireman et al. 2005).

Important abiotic stresses include salinity and heavy metals pollution, declining availability of good quality water, land degradation, and extreme drought. Such abiotic stresses may result into nutritional imbalances in the plant causing reduction in water uptake and increase in toxicity, thereby decreasing the value of the grain. A report by Kukreti (2016) revealed that crop failures in India due to salinity were estimated at approximately 8.6 million per ha. Salts and heavy metals affect the metabolic, physiological and biochemical activities, subsequently inhibiting growth. A reduction in finger millet yield of about 40% has been estimated in both arid and semi-arid areas due to water scarcity.

There are seven major diseases of finger millet namely; blast, seedling blight, wilt or foot rot, Cercospora leaf spot, downy mildew or green ear disease, smut and damping-off (Anilkumar et al. 2003). Finger millet leaf blast (*Magnaporthe grisea*) (T. T. Hebert) M. E. Barr (anamorph *Pyricularia grisea*) was first reported in India, from Tanjore delta of Tamil Nadu by McRae (1920). It affects the leaf, neck and fingers of grown finger millet and causes recurring yield losses. Seedling blight or leaf blight, which was first spotted in India, is caused by *Drechslera nodulosum* (Butler 1918), and is next only to blast in terms of severity and distribution. The other finger millet diseases include *Sclerotium rolfsii* (Coleman 1920), resulting to up to 50% yield loss; Cercospora leaf spot, which causes ear malformation (Pradhanang 1994); smut disease (*Ustilago eleusine*) (Kulkarni 1922) and dumping off disease caused by *Pythium aphanidermatum* (Mehta and Chakravarty 1937).

The most important biotic constraints in finger millet are blast disease and the parasitic weed called *Striga hermonthica.* The blast fungus infects finger millet at all growth stages, causing major losses through neck and panicle infections (Babu et al. 2013). *Striga hermonthica* is specific to African production systems and is considered the greatest biological constraint to food production in sub-Saharan Africa, a more serious problem than insects, birds and plant diseases.

7.2.1 Salinity Tolerance

Finger millet is considered to have a high degree of salt tolerance in comparison to other cereals (Bray et al. 2000; Shailaja and Thirumeni 2007; Rahman et al. 2014). Rahman et al. (2014) undertook a comparison of rice and finger millet accessions in response to salinity and reported superior levels of salinity tolerance in finger millet. Nevertheless, extremely high levels of salinity have been reported to affect the crop's phenology, plant height, shoot biomass and grain yield (Onkware 1986; Krishnamurthy et al. 2014). Natural variation for salinity tolerance among finger millet accessions has been detected through screening of different genotypes under different salinity conditions. At ICRISAT, Krishnamurthy et al. (2014) screened a mini-core collection of 80 finger millet accessions for tolerance to salinity and observed genotypic variation for grain yield, phenology, and shoot biomass. Shailaja and Thirumeni (2007) observed variation among 19 genotypes for their reaction to salt stress.

Rahman et al. (2014) used RNA sequencing of two finger millet genotypes with contrasting response to salinity stress and identified some of the obvious salinity candidates including four aquaporin proteins, sodium/calcium exchanger protein, transporters, signal transducers, and several stress-related transcription factors. In particular, they identified a NAC (no apical meristem) protein (*EcNAC67*) that exhibited differential salinity responsive expression pattern. In a follow-up study, Rahman et al. (2016) undertook functional validation of *EcNAC67* in a rice cultivar ASD16 using *Agrobacterium*-mediated genetic transformation. They confirmed enhanced tolerance against drought and salinity stress. The transformed plants possessed higher relative water content and less reduction in grain yield in comparison to controls. Another *EcNAC1* protein was isolated from finger millet and overexpressed in rice (Ramegowda et al. 2012). The transgenic rice harboring *EcNAC1* proteins were reported to show enhanced tolerance to several abiotic stresses including salinity. More focused studies coupled with functional validation of similar genes have been hindered by the low levels of genetic transformation success in finger millet.

7.2.2 Drought Tolerance

Although finger millet is known to have tolerance to drought, the yield is significantly compromised under extreme drought conditions. Drought stress has been demonstrated to not only cause wilting and leaf rolling in finger millet, but also results in the reduction of leaf solute potential and chlorophyll content with the induction of many drought stress responsive genes (Parvathi et al. 2013). Natural variation for drought stress has been observed in finger millet (Neshamba 2010; Krishnamurthy et al. 2016) although the mechanism of various responses is not entirely known. Puranik et al. (2011) suggested that tolerance to drought might be

attributed to an efficient antioxidant potential and increased signal perception in foxtail millet. In response, Bhatt et al. (2011) screened five finger millet varieties against drought and in parallel studied their antioxidant potential. They observed a positive correlation between drought tolerance and the capacity of finger millet variety PR202's antioxidant system to scavenge reactive oxygen species, resulting in a reduced incidence of oxidative damage (Bhatt et al. 2011). When finger millet was further evaluated for its association with arbuscular mycorrhiza (*Rhizophagus intraradices*) and endophyte (*Piriformospora indica*) under drought stress, an enhanced tolerance to drought was observed through a stronger antioxidant defence system, high chlorophyll content and an enriched osmoregulatory network (Tyagi et al. 2017).

The expression of a finger millet dehydration (dehydrin) gene, *EcDehydrin7*, in transgenic tobacco conferred tolerance to drought stress (Singh et al. 2015). Dehydrins are part of a large group of Late Embryogenesis Abundant (LEA) proteins (Rorat 2006), which have been speculated to protect cells against damage caused by cellular dehydration (Ingram and Bartels 1996; Graether and Boddington 2014). Using transcriptomics in finger millet, LEA proteins were recently (Hittalmani et al. 2017) found to be among some of the upregulated genes under low moisture stress in comparison to well-watered conditions. A genome-wide analysis of rice dehydrin family revealed that these genes play an important role in combating dehydration stress (Verma et al. 2017). A more focused study with the aim of understanding the mechanism of drought tolerance and genes involved will go a long way in helping enhance drought tolerance in finger millet and subsequently mitigating the effects of climate change.

7.2.3 Striga hermonthica

The genus *Striga* has over 30 species that occur naturally in most parts of the world (Scholes and Press 2008). The most important *Striga* species for finger millet production is *S. hermonthica*. *Striga* is a parasitic weed to many cereals including maize, sorghum and rice. There are limited studies on the biology of finger millet-*S. hermonthica* interactions and the mechanism of response to *Striga* remains unknown. A major control measure that has been developed to manage *Striga* is the push–pull technology (Midega et al. 2010). The push–pull technology involves the intercropping of cereals with a trap crop (pull), usually Napier grass (*Pennisetum purpureum*), and a forage legume, usually desmodium (*Desmodium* spp.), as a push crop (Khan et al. 2011). Due to the lack of use for desmodium by farmers, the adoption of the push-pull technology has been quite low. Traditionally, farmers have managed *Striga* in cereal fields through intercropping (Aasha et al. 2017) and crop rotations (Oswald and Ransom 2001) with edible legumes such as common bean (*Phaseolus vulgaris* L.), pigeonpea (*Cajanus cajan* (L) Millsp.) and mung bean (*Vigna radiata* (L.) R. Wilczek).

Striga will only germinate upon stimulation by a strigolactone induced by the host plant. Strigolactones are plant hormones that play an important role in plant development. In the case of *Striga*, strigolactones trigger seed germination through receptors called KARRAKIN-INSENSITIVE 2 (KAI2)/HYPERSENSITIVE TO LIGHT (HTL) (Waters et al. 2012; Toh et al. 2015). In sorghum, low germination stimulant (LGS) activity has been exploited for crop improvement with positive results (Gobena et al. 2016). Certain legumes, which are non-hosts to *Striga*, have also been known to induce the germination of *Striga* leading to the death of the germinated *Striga* plants (Odhiambo et al. 2011) as a result of lack of attachment of the *Striga* to the non-host plant. This phenomenon leads to the "suicidal death" of *Striga* and has been used, to some extent, in the control of *Striga,* and especially in the reduction of the seed banks (Fernández-Aparicio 2012).

Despite the limited studies on *Striga*-finger millet interactions, a lot can be learned from other grasses in the management of *Striga* in finger millet fields. Relevant populations will need to be developed to enable the understanding of various mechanisms involved in response to *Striga*. Better characterization of *Striga* should be done in order to establish whether there is gene-for-gene resistance as has been reported in cowpea (Li and Timko 2009). Wild relatives of finger millet will be valuable and should be screened alongside the landraces and cultivated accessions while looking for novel sources of resistance to *Striga*.

7.2.4 Blast Disease

Blast disease has been reported in all finger millet growing regions and is by far the most devastating disease in finger millet. *M. grisea* parasitizes several economically important grasses; destroys rice crops worldwide and now threatens global wheat production (Wang and Valent 2017). Blast disease affects the leaf, neck, and fingers of grown finger millet and can also cause seed discoloration (Panwar et al. 2011). Neck and finger blast are the most destructive forms of the disease (Takan et al. 2012). Studies done in India using isolates from finger millet and rice confirm that the rice- and finger millet-infecting blast populations are distinct (Viji et al. 2000; Takan et al. 2012). Pathogen genetic groups have been reported within finger millet blast populations (Takan et al. 2004; Shanmugapackiam et al. 2015), although there could be regional distinctness. For example, the presence of the *grh* element has been observed in collections from Japan, India and Nepal (Dobinson et al. 1993) and not from Africa. However, there seems to be new introductions of the *grh* element in the east African region (Takan et al. 2004).

In rice, more than 100 *R* genes (Su et al. 2015; Zheng et al. 2016) have been identified and $\sim$500 quantitative trait loci (QTLs) have been mapped for resistance to blast (Ashkani et al. 2016). Most of the *R* genes have been identified in landraces

(Umakanth et al. 2017) or from wild rice species (Das et al. 2012) and most of them belong to the nucleotide-binding site—leusine rich repeat (NBS-LRR) family. Applying the same knowledge to identify resistance genes in finger millet, some functional markers have been developed using comparative genomics (Panwar et al. 2011; Babu et al. 2014a). Association mapping in finger millet has also been attempted but due to limited numbers of markers, the QTLs identified were not highly significant (Babu et al. 2014a; Ramakrishnan et al. 2016). With the availability of the whole genome sequence (Hittalmani et al. 2017; Hatakeyama et al. 2017) and the abundant genetic resources available in gene banks for finger millet, it should be possible to identify major genes and QTLs for blast resistance. Proper characterization of the pathogen will also be required to ensure the mode of resistance in different resistant genotypes is clearly understood.

7.3 Genetic Resources for Climate Smart Traits

East Africa and India are considered the primary and secondary centers of diversity respectively (Bisht and Mukai 2001) for finger millet. Eight species, namely, *E. coracana, E. kigeziensis, E. indica, E. multiflora, E. floccifolia, E. intermedia, E. jaegeri* occur in East Africa (Philips 1972). *E. tristachya* is endemic to South America (Philips 1972; Devarumath et al. 2005; Neves et al. 2005). Most of the *Eleusine* species are quite localized except *E. indica*, *E. coracana E. tristachya* and *E. multiflora. Eleusine indica,* also known as gooseberry, is considered one of the top ten worst weeds worldwide (Holm et al. 1977). *E. tristachya* has spread from South America to North America, Australia, Africa and Europe (Hilu 1980; Agrawal and Maheshwari 2016). There is also a recent publication reporting the identification of *E. multiflora* in India (Prabhukumar et al. 2017). The primary gene pool of *Eleusine* consists of all the varieties and landraces of the cultivated *E. coracana* subsp. *coracana*. *Eleusine coracana* subsp. *africana* form the major part of the secondary gene pool as well as any other cross-compatible wild taxa (Agrawal and Maheshwari 2016). All other wild *Eleusine* species belong to the tertiary gene pool.

More than 37,000 wild and cultivated finger millet germplasm has been conserved globally (Vetriventhan et al. 2016) in various gene banks, with the National Bureau of Plant Genetic Resources in India having the highest number of collections (>10,000) followed by ICRISAT (7519). The majority of ICRISAT collections are landraces (7121) with only 205 wild accessions, 143 improved varieties and 50 breeding lines. There are significant collections in Kenya, Uganda, Tanzania, Ethiopia and other neighboring countries (Table 7.1). ICRISAT established a core collection consisting of 622 accessions using 14 quantitative traits (Upadhyaya et al. 2006) and later narrowed this set down to a mini-core collection consisting of 80 accessions (Upadhyaya et al. 2010). Unfortunately, wild accessions are only 5% of all the global collections (CROP TRUST 2012). There is limited use of wild relatives

Table 7.1 A summary of finger millet collections in various countries

Source	No. of collections	Source	No. of collections
ICRISAT	7519	Tanzania	293
USDA (Georgia)	766	Malawi	145
India (genebank)	10,507	Eritrea	120
Nepal	877	Burundi	113
Sri Lanka	393	Ethiopia	71
Bhutan	84	Nigeria	20
Kenya	1902	South Africa	17
Zimbabwe	1158	China	300
Uganda	1155	Russia	110
Zambia	497	Vietnam	52

Source: Summarized from CROP TRUST (2012) ICRISAT record updated from http://genebank.icrisat.org/

in finger millet improvement, except for a currently funded CROP TRUST project in Kenya focusing on the identification of novel genes for resistance to *S. hermonthica* and blast disease from wild relatives. There have been on-going efforts to undertake more expeditions within eastern Africa to collect the vast genetic resources. Bio-Innovate Africa (https://bioinnovate-africa.org/about-us/) recently supported the collection of wild finger millet germplasm in Kenya, Uganda, Tanzania and Ethiopia with great success. In order to identify gaps in collections and the challenges faced for conservation and use of finger millet, the CROP TRUST developed a "Global Strategy for the ex situ Conservation of Finger Millet" in 2012 (file:///Users/dodeny/Downloads/Finger-Millet-Strategy-FINAL-14May2012%20(1).pdf).

Large genetic variation was reported when the mini-core collection at ICRISAT was screened for response to salinity (Krishnamurthy et al. 2014) and drought stress (Krishnamurthy et al. 2016). Genetic diversity analyses of finger millet germplasm from various genebanks revealed a narrower genetic base within the cultivated accessions as compared to wild species (Salimath et al. 1995; Gimode et al. 2016), perhaps due to the self-crossing nature. A distinct clustering between Asian and African germplasm has also been reported in several studies (Dida et al. 2008; Arya et al. 2013; Ramakrishnan et al. 2015). This suggests that higher heterosis is likely to be achieved when crosses are made between Asian and African germplasm. Hybridization based breeding has been going on between Uganda and India since the late 1960s and has led to the release of "*Indaf*" varieties (Dida et al. 2008) with improved yields. In order to efficiently broaden the genetic base and significantly improve the performance of this crop, breeders will need to exploit the different centers of diversities and different genepools in their breeding programs.

7.4 Genetic Mapping in Finger Millet

Genetic mapping in finger millet is in its infancy in comparison with other major cereals like maize, wheat and rice. The first partial finger millet genetic map was constructed by Dida et al. (2007) using restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP) and single strand conformation polymorphic (SSCP) expressed sequenced tags. The map covered the nine homoeologous chromosome groups and was constructed using an interspecific F_2 mapping population between *Eleusine coracana* subsp. *coracana* (Okhale 1) and *Eleusine coracana* subsp. *africana* (MD-20). The map contained 327 loci that were mapped to either A or B genomes. One hundred and thirty one (131) markers covered 721.4 cM of 16 linkage groups that were mapped on the A genome. The remaining 196 markers covered 786.8 cM of nine linkage groups of the B genome. More recently, a more robust single nucleotide polymorphism (SNP) linkage map was developed using $F_{2:3}$ families of the same interspecific cross between Okhale 1 and MD-20 (Qi et al. 2018). They mapped 4,453 SNP markers in 18 linkage groups that were designated the same as in Dida et al. (2007) and incorporated a subset of markers that had been mapped in the first linkage map. This linkage map is a significant contribution to finger millet genetics research, especially if it can be used to anchor the whole genome sequence (Hittalmani et al. 2017; Hatakeyama et al. 2017). Future efforts will still need to focus on generating intraspecific maps within the primary gene pool.

The low number of markers has resulted in limited association mapping studies in the past, although some reports are available, especially for association of markers with agro-morphological characters (Table 7.2). Using 113 accessions screened in two sites in India, Sharma et al. (2018) reported significant SNP associations with 14 agro-morphological traits at a p value threshold of $p < 0.01$ and $p < 0.001$. Lule et al. (2018) reported 16 associations between 13 microsatellite markers and six agronomic traits at $p < 0.01$. Babu et al. (2014b) used 46 simple sequence repeats (SSRs) and reported the association of five markers with four agronomic traits (basal tiller number, days to 50% flowering, flag leaf width and plant height) at $p < 0.01$ and $p < 0.001$. Babu et al. (2014a) developed genic SSRs and used 104 markers to detect four QTLs for finger blast and one QTL for neck blast resistance. Two QTLs were found to be associated with tryptophan content and one QTL for protein content in a study aimed at identifying alleles responsible for *opaque2* modifiers (*Opm*) (Babu et al. 2014c). All these mapping studies used relatively low numbers of accessions and extremely low numbers of markers (except in the study by Sharma et al. 2018). Although none of these QTLs has been validated, the recent availability of the whole genome sequence provides more opportunities for using high-throughput markers for association mapping studies.

Comparative mapping of finger millet has been done with rice (Srinivasachary et al. 2007), which revealed high levels of colinearity. A recent phylogenetic study using single copy orthologous genes among closely related grasses confirmed the close relationship between finger millet and rice (Hittalmani et al. 2017). A more

Table 7.2 A summary of QTLs detected in various studies in finger millet using association mapping

Study reference	Traits analysed	Population	QTL identified	P-value cut-off
Sharma et al. (2018)	Days to 50% flowering; Days to maturity; Basal tiller no.; Plant height; Culm thickness; Flag leaf blade length; Flag leaf blade width; Peduncle length; Ear length; Ear width; Length of longest finger; Width of longest finger; Finger number per ear; Grain yield	113 diverse accessions	Several	$P < 0.01$
Lule et al. (2018)	Days to maturity; Finger number; Grain yield per plant; Number of grain per spikelet; Productive tiller number; Thousand grain weight	138 diverse accessions	Several	$P < 0.01$
Babu et al. (2014b)	Basal tiller number; Days to 50% flowering; Flag leaf width; Plant height	190 diverse accessions	Several	$P < 0.01$; $P < 0.001$
Babu et al. (2014a)	Finger blast; neck blast	190 diverse accessions	5 QTLs	$P < 0.01$; $P < 0.001$
Babu et al. (2014c)	Tryptophan content; protein content	190 diverse accessions	2 QTLs	$P < 0.01$; $P < 0.001$

detailed whole genome comparison between finger millet and other grasses will be necessary, not only to confirm the unique structural rearrangements reported by Srinivasachary et al. (2007), but also to understand the genomic relationships between finger millet and other grasses.

7.5 Genomics-Assisted Breeding

Whole genome sequences of three finger millet genotypes PR202 (Hatakeyama et al. 2017), ML365 (Hittalmani et al. 2017), and KNE796 (unpublished data) are available online. There is a consensus in genome size (1.5 Gbp) and GC content of the three genomes although differences prevail in numbers and sizes of the protein coding genes (Table 7.3). The reported gene numbers by Hittalmani et al. (2017) for ML365 and Hatakeyama et al. (2017) for PR202 (Table 7.3) will further need to be re-analyzed in order to come up with a consensus number. A preliminary genome sequence comparison of finger millet with other cereals revealed 95%, 90% and 65% collinear blocks with rice, maize and sorghum, respectively. A large number of genes in finger millet genome form core gene families with other cereal

Table 7.3 Statistics of published finger millet genomes

Source	PR202	ML365
Protein-coding gene number	62,348	85,243
Mean gene length (kbp)	2.50	2.06
Total CDS length (mbp)	68.66	75.38
Mean CDS length (kbp)	1.07	0.88
Number (%) of single-exon genes	16,210	26,449
GC content	43.9	44.9
Repeat content (% of genome)	N/A	49.9

species. In total 9,896 core orthologous groups (COGs) of gene families are shared by rice, maize, sorghum, pearl millet and foxtail millet.

7.6 Climate Smart Genes in the Finger Millet Genome

According to drought stress gene database, 78 genes have been categorized for physiological adaptation under drought stress (Alter et al. 2015). We identified 52 out of the 78 genes in the finger millet genome (Table 7.4), out of which 37 are known to be involved in osmoregulation to balance the ionic and osmotic homeostasis, 12 for detoxification, and three for growth control in plants. For example, *ABCG25* gene is reported to be involved in abscisic acid (ABA) transport and response (Kuromori et al. 2010) as well as enhancing intercellular ABA signaling in plants (Kuromori et al. 2016). Similarly, many other stress-responsive genes found in the finger millet genome such as *LOS5, CPK4, AB1* and *AB2* have been reported

Table 7.4 Genes involved in physiological adaptation in plants under stress conditions

Biological process	Gene	FM ID	Function
Ion and osmotic homeostatis			
	AAO3	N.D	Arabidopsis aldehyde oxidase
	ABCG25	ECOR024010	ABC-transporter, ABA export from cells
	ABCG40	N.D	ABC-transporter, ABA import
	ABH1/CBP80	ECOR006018	Subunit of mRNA cap-binding complex
	ABI1	ECOR033624	Protein phosphatase 2C 56
	ABI2	ECOR049722	Protein phosphatase 2C 77
	ABO1/ELP1	ECOR038014	Subunit of Elongator
	AQP1/TIP1-1	ECOR020980	PIP1 plasma membrane aquaporin
	BG1/BGLU18	ECOR017856	Beta-glucosidase; hydrolyzes glucose-conjugated
	ATHB6	N.D	Homeodomain protein, target of ABI1
	AtrbohD	N.D	NADPH oxidase catalytical subunit
	CBP20	ECOR002984	Cap Binding Protein 20

(continued)

Table 7.4 (continued)

Biological process	Gene	FM ID	Function
CLC-C		ECOR020329	Chloride channel
CPK4		ECOR032246	Calcium-dependent protein kinases
CYP707A1		N.D	ABA catabolism; 8'-hydroxylation of ABA
CYP707A3		ECOR014044	ABA catabolism; 8'-hydroxylation of ABA
DOR		ECOR006224	Drought tolerance repressor, F-box protein
DRB1/HYL1		ECOR009359	Hyponastic leaves 1; RNA binding protein that affects ABA and drought sensitivity
DSM2		N.D	Put. beta-carotene hydroxylase, ABA biosynthesis
GCR1		ECOR045780	Putative G protein-coupled receptor
GORK		N.D	Outward K + channel
GPA1		ECOR028625	Alpha subunit of heterotrimeric GTP-binding protein
GTG1		ECOR036005	PM-ABA receptor, GPCR-type G protein
GTG2		N.D	PM-ABA receptor, GPCR-type G protein
HAB1		N.D	Protein phosphatase 2C 16
KAT2		ECOR033046	K+ channel, inward rectifying
LHCB6		N.D	Light harvesting chlorophyll a/b binding protein
LLA23		N.D	ABA-, stress-, and ripening-induced protein
LOS5/ABA3		ECOR026538	Molybdenum-cofactor sulfurase
MRP4		ECOR012433	Multidrug resistance-associated protein, ABC transporter
NADP-ME1		ECOR009538	NADP-malic enzyme
NCED1		ECOR034474	ABA biosynthesis
NCED3		ECOR042900	ABA biosynthesis key enzyme
OST1/SRK2E		ECOR033474	Kinase-like (open stomata 1), activated by ABA, activates SLAC1
OST2/PMA1		ECOR043481	Plasma membrane proton ATPase
PCKA/PEPCK		ECOR005523	PEP carboxykinase
PED1/KAT2		ECOR038688	3-ketoacyl-CoA thiolase 2
PIP1-1		ECOR032142	Aquaporin
PIP1-4		N.D	Probable aquaporin
PIP2-1		ECOR047129	Aquaporin
PIP2-2		ECOR013882	Aquaporin
PIP2-5		ECOR017811	Aquaporin
PYL9/RCAR1		N.D	Soluble ABA receptor interacts with and regulates PP2Cs ABI1 and ABI2
RBOHF		ECOR039003	NADPH oxidase catalytical subunit
RFP1/SDIR1		ECOR022569	RING-finger protein
RWC3		N.D	Aquaporin
SAD1/LSM5		ECOR001752	Supersensitive to ABA and drought 1

(continued)

Table 7.4 (continued)

Biological process	Gene	FM ID	Function
SLAC1		ECOR033474	Kinase-like (open stomata 1), activated by ABA
SLAH3		ECOR050224	Guard cell S-type anion channel (SLAC1 homolog)
SYP61/OSM1		ECOR000072	Osmotic stress-sensitive; related to mammalian syntaxin
TIP2-2/SITIP2-2		ECOR043324	Probable aquaporin
ACS6		N.D	ACC synthase, first step in ethylene biosynthesis
Growth control			
ANN1		ECOR039452	Annexin1
APX		ECOR040940	Ascorbate peroxidase
EVP1		N.D	Vacuolar pyrophosphatase
HDG11/ROC8		ECOR011713	Enhanced drought tolerance1, HD START TF
RGS1		N.D	Regulator of G-protein signaling
Detoxification			
Osmolyte production			
ADC1		ECOR016738	Arginine decarboxylase; polyamine biosynthesis
CMO		ECOR024646	Choline monooxygenase; glycine betaine biosynthesis
FSPD1/SPDSYN1		ECOR051004	Spermidin synthase
GOLS1		N.D	Galactinol Synthase
GOLS2		ECOR005876	Galactinol Synthase
IMT1		N.D	D-myo-inositol methyltransferase
MYB4		ECOR031142	MYB TF
P5CS		N.D	Pyrroline-5-Carboxylate Synthase; glutamtate → proline
P5CS1/P5CSA		ECOR002007	Pyrroline-5-Carboxylate Synthase; glutamtate → proline
SAMDC		ECOR006068	S-adenosyl methionine decarboxylase, Polyamin synthesis
TPS1		ECOR008673	Trehalose-6-phosphate synthase
Removal of ROS			
APX2		ECOR025343	Ascorbate peroxidase 2, H_2O_2 scavenger
ERD1/CLPD2		ECOR034553	Chloroplast-targeted Clp protease reg SU
GhMT3a		N.D	Metallothionein, ROS scavenger
GPX3		N.D	Glutathione peroxidase3
GSTU17		ECOR035212	Glutathion s-transferase U17
PO2		N.D	Extracellular peroxidase 2
SODCP		ECOR009244	Superoxide dismutase
Protection factor			
HVA1		N.D	Late embryogenesis abundant protein, group 3
TaLEA		N.D	Late embryogenesis abundant
TAS14		N.D	Dehydrin, group2 LEA proteins

to be involved in ABA synthesis and are considered to be important players in abiotic stress tolerance (Meyer et al. 1994; Rodriguez et al. 1998; Xiong et al. 2002).

We also observed several genes involved in growth and development, which have been reported to play a role in stress tolerance. For example, *Annexins,* which act as targets of calcium signals (Mortimer et al. 2008), have been reported to play an important role during growth (Blackbourn et al. 1992; Clark et al. 1992; Carroll et al. 1998). In *Arabidopsis thaliana*, upregulation of *ANN1* (Annexin 1 protein) during abiotic stress conditions was shown to reduce hydrogen peroxide accumulation in guard cells leading to more tolerance to drought as compared to knockout plants (Konopka-Postupolska et al. 2009). A putative homolog of *HDG11*, which encodes for a homeodomain (HD)-START family transcription factor, has also been detected in the finger millet genome. The induction of *HDG11* gene has been shown to increase root growth and reduced stomatal density as well as drought and osmotic stress tolerant characteristics in *Arabidopsis* and other plants (Yu et al. 2008; Zhu et al. 2016; Yu et al. 2016).

There will be need to study these genes individually in finger millet in order to determine their specific roles under various stresses. However, this will need to be done after an improved and anchored assembly and annotation of the genome has been accomplished.

7.7 Future Perspectives

Finger millet remains an important cereal crop in the semi-arid tropics and is likely to gain more importance as more genomic resources become available and more people show interest in healthy eating. The high demand for finger millet in dry areas will require the release of better yielding varieties coupled with unique resistance to biotic and abiotic stresses. The current largely conventional breeding approaches in finger millet will not be sufficient if the full potential of the crop is to be realized. With the availability of a draft whole genome sequence, research will need to focus on characterizing important traits and utilizing genomics-assisted breeding for more efficient release of superior varieties. There is a great opportunity to implement genomic selection in finger millet and breeders will need to work alongside bioinformatics specialists in order to make available the necessary genetic and genomic resources that will enable accurate and more efficient breeding in this unique climate smart crop. Both secondary and tertiary gene pools will be of great value as sources of novel genes and for broadening the genetic base of the crop.

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