Chapter 3
Finger Millet (*Eleusine coracana* L. Gartn.) Breeding

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Abstract Finger millet (*Eleusine coracana* (L.) Gaertn.) is a minor millet grown in the arid and semiarid tropics and subtropics of Asia and Africa. It is cultivated for food, as well as fodder and medicinal purposes. The genus *Eleusine* includes eight species of diploid and tetraploid annual and perennial herbs. The cultivated species also have several races and subraces and hence, finger millet displays great variability and diversity for most agronomically- important traits. It is a hardy crop which can withstand abiotic stress such as water scarcity and cold temperatures. Several genotypes are blast resistant and nutritionally rich especially in minerals and essential amino acids. Therefore, studying the germplasm diversity and selection of superior genotypes are prerequisites for a successful breeding program for crop improvement. The advent of tissue culture techniques, genomics and transcriptomics will further facilitate the study of genetic diversity. Increasing the finger millet production will help attain food and nutritional security especially for poor countries. Although the Green Revolution has transformed agriculture sector, the shift from traditional to modern production systems has led to the displacement of traditional landraces and genetic erosion of many crop species. It is thus vital to preserve the germplasm for the conservation of genetic diversity. The present chapter reviews the finger millet species, present diversity and recent breeding programs to improve the crop. The chapter also discusses the measures taken for genetic conservation of the species.

Keywords Blast resistant · *Eleusine* · Finger millet · Genomic resources · Improved varieties · Interspecific breeding

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3.1 Introduction

Finger millet or *Eleusine coracana* (L.) Gaertn. (Gaertner 1788; Basionym: *Cynosurus coracanus* Linnaeus) is a minor cereal millet. It is also known as bird's foot millet, coracana, African millet, ragi and kurukkan. The generic name *Eleusine* is derived from *Eleusis* an ancient city sacred to Demeter, the Greek goddess of agriculture. The term *coracana* is derived from its name *kurukkan* in the Sinhalese language of Sri Lanka. The common name finger millet is acquired from the finger-like branching of the panicle. Finger millet is an allotetraploid (2n = 4X = 36), mainly found in the arid and semiarid tropics and subtropics (Fakrudin et al. 2004). It is a robust annual grass grown as a cereal in more than 25 countries in warm temperate regions of Africa, Asia and South America (Phillips 1972). Finger millet is nutritionally comparable to rice and wheat and ranks fourth in importance among millets in the world after sorghum, pearl millet and foxtail millet (Upadhyaya et al. 2007). Around 4.5 million mt of finger millet are produced worldwide every year accounting for 12% of the global millet area (ICRISAT 2015). Africa produces 2.5 million mt and India produces 1.2 million mt annually. Finger millet accounts for about 85% all millets produced in India and is cultivated over 1.19 million ha in India according to a recent report (Sakamma et al. 2018).

Finger millet is cultivated for food, as well as fodder and medicinal uses (Oduori 2005; Phillips 1974). It is a hardy crop that can be grown in very diverse environments and can be stored for very long periods. The long duration cultivars can be grown as a hot weather crop while it can also be grown as a cold season crop using early maturing varieties (Duke 1978, 1979). Finger millet can yield as much as 5000 kg/ha of grain. It is a potentially nutritious crop for the increasing world population. Owing to its purported medicinal properties, finger millet has long been used as a folk remedy in Africa and India for several diseases such as liver disease, measles, pleurisy, pneumonia and small pox (Bachar et al. 2013). Various landraces possess genes for robust growth, early vigor, large panicle size, high finger number and branching and high-density grain as well. It is also reported that finger millet is tolerant to alkali, salt, slope, drought, laterite, disease, fungi, insects, mildew, viruses and pH variation (5.0–8.2) (Duke 1978). Some of the landraces are water-efficient types with high carbon dioxide fixation and low leaf area that could perform well in semiarid climates. Others have genes for tolerance to heat, cold, drought, blast resistance and some also for lodging as well as an ability to mobilize phosphorus and utilize nitrogen efficiently (NRC 1996).

Several finger millet cultivars or genotypes have high dietary fiber content, more than 10% protein and a good source of essential amino acids including tryptophan, cysteine and methionine (Iyengar et al. 1945, 1946; Jideani 2012; Mirza et al. 2014b). The micronutrient density of finger millet is also higher than the staple crops like rice or wheat (Rao and Deosthale 1983). It is rich in minerals such as Mn, Cu, Mg, Se, Mo and P and is particularly high in Ca content (Barbeau and Hilu 1993; Jideani 2012; Mirza et al. 2014a; NRC 1996; Vadivoo et al. 1998). The grains are also rich in vitamin B complex such as thiamine, riboflavin, folic acid and niacin (Gull et al. 2015; Saleh et al. 2013). Due to its reasonably high grain calcium content

and nutritionally good quality, finger millet can be used for formulating diets for pregnant and lactating women as well as for growing children and can be utilized in preventing or lowering the risk of osteoporosis (Antony and Chandra 1998; Poutanen 2012; Verma and Patel 2013). Millet is also recognized for its health benefits such as hypoglycemic, hypocholesterolemic, anti-ulcerative, nephroprotective and anti-cataractogenic characteristics (Chethan and Malleshi 2007; Shobana et al. 2010). Consumption of a finger millet-based diet has been reported to significantly lower plasma glucose levels in hyperglycemic adults suffering from non-insulin dependent diabetes mellitus (NIDDM) (Kumari and Sumathi 2002; Muthamilarasan et al. 2016) attributed to its higher fiber content. Condensed tannins extracted from finger millet have been shown to exert significantly higher antioxidant and anti-diabetic activities than other food ingredients (Kunyanga et al. 2011). Finger millet is regarded as the *wonder grain* due to its excellent nutritional properties and termed a *famine crop* owing to its long storability, ensuring food and nutritional security (Fakrudin et al. 2000; Gupta et al. 2017; Mgonja et al. 2007; Takan et al. 2004). In 2015, ICRISAT added finger millet as its sixth mandate crop.

To design a successful breeding program, it is essential to understand the biology of the plant and identify the existing variability and diversity in the genus. This chapter gives an up-to-date review of the information and resources generated for finger millet including the plant biology, species characterization, wild relatives, and achievements in breeding and transgenic developments. The chapter also details the agricultural limitations related to the crop and recommendations for future research.

3.2 Taxonomy

Finger millet was firstly documented by Linnaeus (von Linnaeus 1759) in *Systema Naturae, Editio Decima II* where he identified it as *Cynosurus coracan* hence, the basionym *Cynosurus coracanus* L. The genus *Eleusine* was later described in detail by Gaertner (1788) in *De Fructibus et Seminibus Plantarum* and hence the appellation, *Eleusine coracana* (L.) Gaertn.

Kingdom:	Plantae
Subkingdom:	Tracheobionta
Superdivision:	Spermatophyta
Division:	Magnoliophyta
Class:	Liliopsida
Subclass:	Commelinidae
Order:	Cyperales
Family:	Poaceae
Subfamily:	Chloridoideae
Genus:	*Eleusine* Gaertner
Species:	*Eleusine coracana* (L.) Gaertn.

The genus *Eleusine* includes nine annual and perennial species as recognized by Phillips (1972), with eight African species and one New World species (*E. tristachya* Lam.) native to Argentina and Uruguay (Lovisolo and Galati 2007). The range of the genus has been extended by widespread introduction of the crop (*E. coracana*) throughout the tropics, and the common weed often associated with cultivation, *E. indica* (L.) Gaertn. East Africa is considered the center of diversity of the genus and eight species (*E. africana, E. coracana, E. kigeziensis, E. indica, E. floccifolia, E. intermedia, E. multiflora and E. jaegeri*) (Table 3.1) occur in this region (Mehra 1963; Phillips 1972). The species of *Eleusine* Gaertn. are distributed in the tropical and subtropical areas (Fig. 3.1) of India, Myanmar, Sri Lanka, Nepal, China and Japan in Asia; while in Africa, it is grown in Uganda, Kenya, Tanzania, Ethiopia, Eritrea, Rwanda, Zaire and Somalia (Upadhyaya et al. 2010). It is an annual allotetraploid (2n = 4X = 36, AABB) that includes two distinct subspecies: *E. coracana* ssp. *coracana* (L.) Gaertn. and *E. coracana* ssp. *africana* (Kennedy-O'Byrne) Hilu & de Wet (Hilu 1994; Hilu and de Wet 1976). *Coracana* is the cultivated ssp. while *africana* is the wild ssp. Wild finger millet is native to Africa and is believed to have migrated from there to Asia and the Americas. The cultivated ssp. *coracana* was domesticated from wild populations of *E. coracana* ssp. *africana* as suggested by morphological and cytogenetic evidence, and through molecular studies (Chennaveeraiah and Hiremath 1974; Hilu and de Wet 1976; Hilu and Johnson 1992). Both cultivated and wild species are important from the point of germplasm collection, conservation and utilization, since they collectively form the primary gene pool. Dida et al. (2008) recently demonstrated the gene flow between ssp. *africana* and ssp. *coracana* through genotypic analysis of microsatellites. However, hybridization between the wild and cultivated populations has given rise to many morphological intermediates that are completely fertile. These hybrids are aggressive colonizers and are grouped under the race spontanea (De Wet et al. 1984; Kennedy-O'Byrne 1957; Mehra 1962; Phillips 1995). The diploid wild species *E. indica* (L.) Gaertn., *E. floccifolia* Spreng. and *E. tristachya* (Lam.) Lam., supposedly form the secondary gene pool while the tertiary gene pool includes *E. intermedia* (Chiov.) S.M. Phillips, *E. jaegeri* Pilg., *E. kigeziensis* S.M. Phillips and *E. multiflora* A. Rich. (Guarino 2012) (Fig. 3.2).

3.2.1 Eleusine coracana *ssp*. africana

The *africana* ssp. is found along the highlands of East Africa and the grasslands of Southern Africa. It has also been reported from India and the UK. *Africana* was first recognized as a distinct species by Kennedy-O'Byrne 1957). Afterwards, considering the morphological similarities, it was designated a subspecies of *E. indica* (Lye 1999; Phillips 1972, 1974). *Eleusine africana* is comparatively robust as compared to *E. indica*, with longer leaves, thicker and longer spikes, larger bracts etc. but has very similar morphology. However, attempts of hybridization between the tetraploid *E. africana* (2n = 4x = 36, AABB) and the diploid *E. indica* (2n = 2x = 18, AA)

Table 3.1 Other *Eleusine* spp. of possible genetic value

Species	Notes	References
Eleusine floccifolia	Perennial diploid (2n = 2x = 18); distinguishing white hairs on leaf margins; mid to high elevations; avoided by livestock	Phillips (1972, 1974, 1995) and Sisay and Baars (2002)
Eleusine intermedia	Perennial diploid (2n = 2x = 18); stout rhizome; softer leaves with sparse, soft straight hairs on the smooth margins (pilose); laxly arranged spikelets; florets with 3-nerved lemmas with distinct 1-nerved keel or ridge	Grassland Index (2009) and Phillips (1972)
Eleusine jaegeri	Perennial diploid (2n = 2x = 20); most robust; common in grasslands of east African mountainous regions; invasive culms branch abundantly form thick and coarse tussocks or tuft; whitish overlapping leaf-sheaths; tough pale green glabrous leaves with rough margins; unpalatable to livestock; used for basket making	Grassland Index (2009) and Phillips (1972, 1974, 1995)
Eleusine kigeziensis	Perennial tetraploid (2n = 2x = 38); occurrence-east African uplands; short slender ascending rhizome; long open inflorescence; fairly soft leaves sometimes pilose lacking hair; lemma with a central and two lateral inconspicuous nerves; distinguishing lemmas with a central 3-nerved keel	Phillips (1972, 1974, 1995)
Eleusine multiflora	Annual diploid (2n = 2x = 16); distinct three or more short oblong-ovate spikes generally at a distance of 1 cm or more from each other alternating at the top	Hilu and Johnson (1997), Neves (2011) and Werth et al. (1994)
Eleusine tristachya	Annual diploid (2n = 2x = 18); only species native to South America; important forage grass; digitate inflorescence tightly clustered at the top of the axis; short and oblong spikes with spikelets neatly arranged perpendicular to the spike axis	Clayton et al. (2006-onwards), Ellis et al. (2004), Hansen (1980), Hilu (1980, 2003), Sanz Elorza et al. (2001), Lovisolo and Galati (2007), Phillips (1972, 1974, 1995) and USDA NRCS (2009)
Eleusine indica	Annual diploid (2n = 2x = 18) known as goosegrass; major weed worldwide; small plant with narrow rachis and thin stems; 3-nerved lemmas with a 3-nerved keel; short shattering spikelets; small seeds enclosed in relatively short glumes and lemma and thin racemes	Phillips (1972) and Neves (2011)

resulted in sterile plants (Channaveeraiah and Hiremath 1974; Hiremath and Salimath 1992). Whereas, it was observed to hybridize ssp. *coracana* in nature and hence classified as a subspecies of *E. coracana*.

Later, studies of chromosome numbers and genome size clearly distinguished *Eleusine africana* from *E. indica*. It is an annual plant that grows in dense tufts. They have geniculately ascending culms and branching at the lower nodes. The inflorescence branch is long and flowering culms are up to 135 cm tall. The inflores-

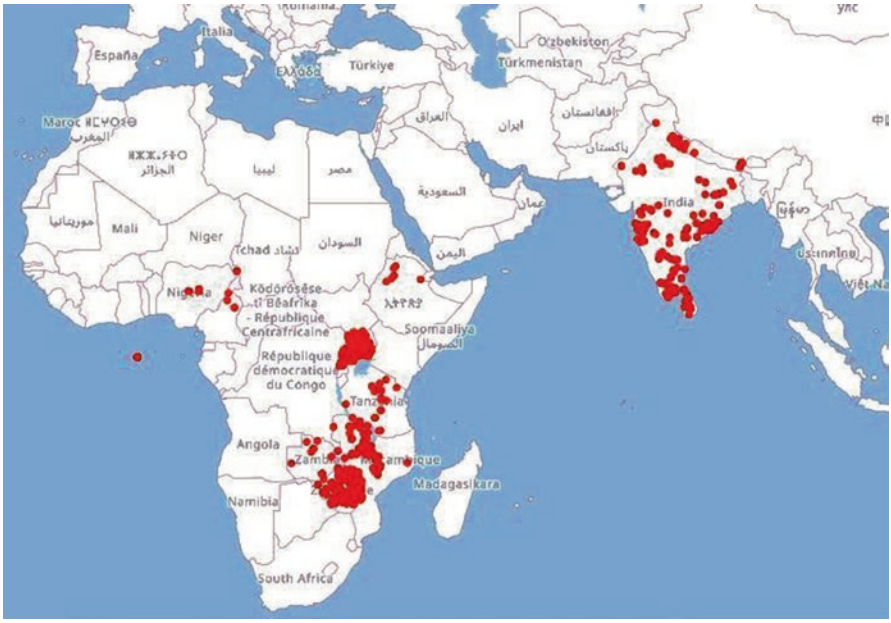

Fig. 3.1 Distribution of *Eleusine* accessions map generated in GENESYS, a global portal to information about Plant Genetic Resources for Food and Agriculture (PGRFA)
Source: https://www.genesys-pgr.org

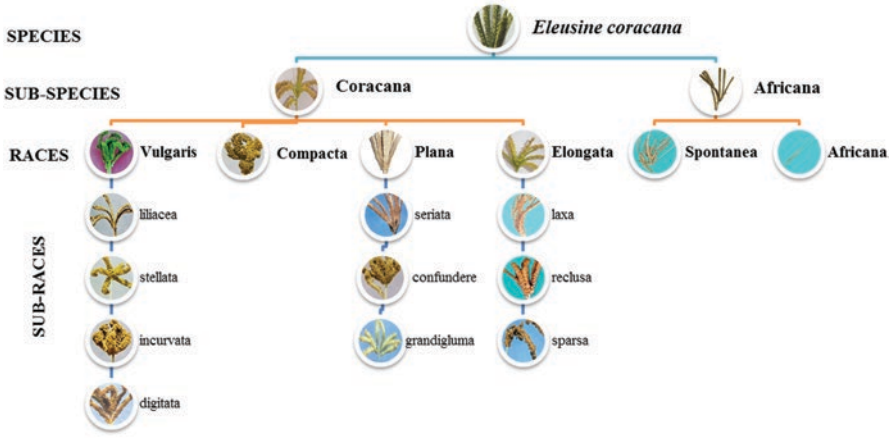

Fig. 3.2 Races and subraces of the species *Eleusine coracana*

cence or spike is long and open. The spikelets are arranged in two rows on one side of the rachis. Glumes are shorter than spikelet, lanceolate-oblong, rarely more than 5 mm and narrow-winged along the keel (Bharathi 2011). The ligule and grain characteristics can differentiate *E. africana* from *E. indica*. In *E. africana*, the ligule has

a clear ciliate fringe while in *E. indica*, the ligule is a truncate, scarcely ciliolate membrane. The *E. africana* grain has very fine granular surface with barely visible ridges whereas in *E. indica,* the grain has well-marked, oblique ridges (Hilu et al. 1979; Phillips 1972). *Eleusine coracana* ssp. *africana* has two races, Africana and Spontanea (Fig. 3.2).

Race Africana is found in Burundi, Uganda, Malawi, Tanzania and Ghana. Plants may be erect, prostrate or decumbent and can reach a height up to 165 cm. Race Africana has the characteristic long open inflorescence. The panicle has 4–14 fingers and a length up to 14 cm. The grains are brown to dark brown in color.

Race Spontanea is found in Kenya, India and also in the UK. The plants are erect and both green and pigmented. The maximum height recorded for Spontanea is 120 cm. The fingers are generally 6–9 cm and incurved. The inflorescence generally consists of 6–8 fingers however, up to 10 fingers have also been reported. The grains can be light to dark brown.

3.2.2 Eleusine coracana *ssp*. coracana

The *coracana* ssp. is an annual tetraploid (2n = 4x = 36, AABB). It includes all the four cultivated races (elongata, plana, compacta, vulgaris) and subraces (Fig. 3.2) that show considerable morphological variation of the inflorescence and more frequently referred simply as *E. coracana* (De Wet et al. 1984; Dida and Devos 2006; Hilu and de Wet 1976; Upadhyaya et al. 2007). The morphological characteristics of the each of the subraces are discussed below (Bharathi 2011).

Plants are annual, erect or geniculately ascending culms and can reach a height of 165 cm high (Fig. 3.3). Culms are commonly branched from the upper nodes to produce secondary inflorescences. Inflorescences are difitate or subdigitate, often with one or more racemes some distance below the main cluster of 4–19 branches.

Fig. 3.3 *Eleusine coracana* ssp. *coracana*

Inflorescence branches are slender to robust sometimes with secondary branches. Each spikelet comprises of 6–9 overlapping flowers which are 6–10 mm long and mostly arranged in two rows along one side of the rachis. It is unique in its grain characteristic as it bears a utricle instead of a true caryopsis like other cereals (McDonough et al. 1986a). The globose grains (after removal of the pericarp) may be blackish, brown, reddish or even whitish while the grains of other *Eleusine* species are typically blackish (Phillips 1972, 1974, 1995). The grains are exposed between the florets in the nonshattering spikelets, when ripe whereas in other *Eleusine* species (including ssp. *africana*), spikelets dis- articulate (between the florets) at maturity and grains remain enclosed (Chen and Phillips 2006; Chennaveeraiah and Hiremath 1973; Phillips 1972, 1995).

3.2.3 Eleusine coracana *ssp.* coracana*, Races and Subraces*

Race *Elongata* Of the four races, Elongata is morphologically the most distinct (Rao et al. 1993). It is grown in India, Nepal, Zimbabwe, Nigeria, Uganda and South Africa. Plants can grow to be erect or decumbent. The inflorescence is digitate. Spikelets are long, slender, spreading and become curved during maturity (Fig. 3.2). The grains are of different colors, from light brown to reddish and dark brown. It comprises 3 subraces, laxa, reclusa and sparsa. In laxa*,* both erect and decumbent plants are found. The spikelets are arranged in narrow rows on the inflorescence branches, like the wild race Africana*.* It has 5–11 open and long fingers (up to 19 cm) that can be top curved or incurved. Reclusa has comparatively short fingers (12 cm) and are open or top curved. The panicle branches are 5–11 with fingers as long as 12 cm. Sparsa inflorescences are generally pendulous (drooping). It has long fingers up to 14.8 cm and the branches are quite numerous (7–13).

Race *Plana* This race is found in India, Zimbabwe, Kenya, Nigeria, Uganda and Ethiopia. Plants are either erect or decumbent. Plants are green and pigmented. Large spikelets (6–17 cm) arranged in two or more rows along the rachis giving the inflorescence branch a flat ribbon-like appearance is characteristic to this race. Plana also comprises 3 subraces: seriata, confundere and grandigluma (Fig. 3.2). Spikes are mostly top curved in seriata with 6–15 fingers, however, short open are also reported. The grains are light brown, reddish brown to dark brown. In confundere, the spikes are top curved and generally has 6–7 fingers. But, number of panicle branches as high as 23 have been reported from Uganda. The fingers surround the rachis at maturity, giving a compact look to the panicle. The grains are mostly reddish brown. The grandigluma subrace, the spikes are again top-curved with 5–10 fingers, generally is characterized by long, pointed glumes and very long fingers up to 17 cm. The grains are light brown to reddish brown.

Race *Vulgaris* is mostly cultivated in Asia. Plants are both green and pigmented. They show both erect and decumbent growth habit. They can have 5–14 spikelets

(generally 6–8) and the tips are generally in-curved (Fig. 3.2) giving the inflorescence a semi-compact appearance at maturity (Guarino 2012). The fingers are generally 7–10 cm long. It has four subraces. The fingers are in-curved in both stellata and incurvata subraces, more in subrace *incurvata* giving it a fist like appearance. The grains of both subraces are mostly reddish brown or ragi brown. The fingers are reflexed or short open in subrace liliacea while top-curved in subrace digitata. The grains are ragi brown, reddish brown to dark brown, mostly dark brown in subrace digitata.

Race *Compacta* It is mostly found in India, Kenya and Uganda. The members of this race are generally referred to as *cockscomb* finger millet in both Africa and Asia. The erect or decumbent plants are both green and pigmented. The inflorescence axis is divided at the base ascending and the fingers (4–11) are in-curved at the top to give large fist-like appearance (Fig. 3.2). The grains can be light brown, reddish or dark brown in color.

3.3 Breeding Biology

Eleusine coracana is a self-pollinated member of family Poaceae and subfamily Chloridoideae. Cross-fertilization by wind or insects is reported to contribute less than 1% (Seetharam 1998). Since then, several groups have described the genus and floral biology in finger millet (Ayyangar 1932; Ayyangar and Wariar 1934; Chavan and Shendge 1957; Chavan et al. 1955; Coleman 1920; Dodake and Dhonukshe 1998; Gupta et al. 2011; Phillips 1972; Rachie and Peters 1977). Different parts and stages of developing inflorescence have been recently documented in Mirza et al. (2014a). Four principal growth stages (S1, S2, S3, S4) were identified for the developing spike based on a decimal code developed by Zadoks et al. (1974), as shown in Fig. 3.4.

The stage when about one fourth of the inflorescence has emerged is designated as S1 and called the *booting* stage. The inflorescence is light green in color, the spikelets in the fingers are compactly arranged and florets are not identifiable at this stage. The second stage is anthesis stage. The stage when anthesis is halfway is designated as S2 stage. The inflorescence appears yellowish due to the emergence of anthers. The florets became clear. The S3 stage is the grain-filling stage. It is the late milk stage, once increase in solids in liquid endosperm is notable, when the caryopsis is crushed between fingers. The inflorescence and the developing grains are green in color. The developing grains became swollen but remain covered with lemma and palea. In the S4 stage, 50% of spikelets have ripened and the caryopsis has hardened enough so that it is difficult to divide by thumb-nail. The inflorescence is dried, its color changes to yellow-brown and the grains are clearly visible between the gaped florets (Fig. 3.5g).

The Finger millet inflorescence or spike consists of a whorl with 2–11 (average 5–7) digitate, slightly curved or straight spikes or fingers, with an odd one a little

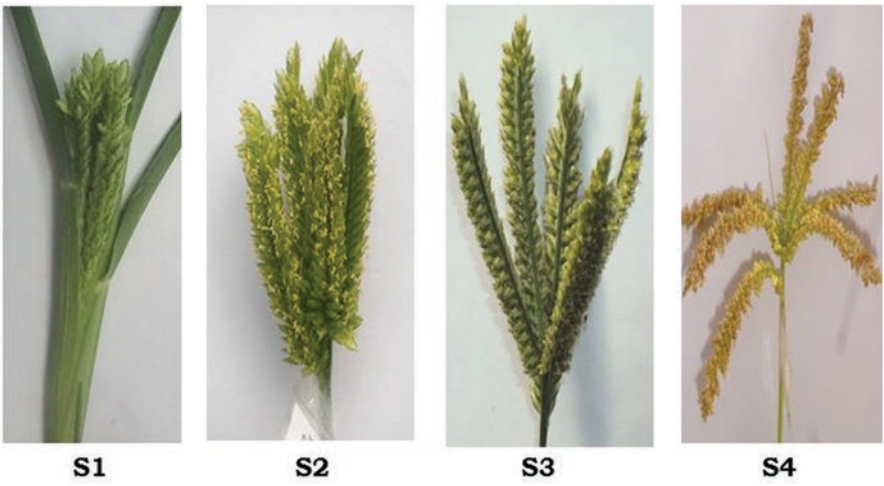

Fig. 3.4 Principal growth stages of the developing finger millet spike. **S1** Booting stage, **S2** Flowering or anthesis stage, **S3** Grain-filling, **S4** Ripening stage
Source: Mirza et al. (2014a)

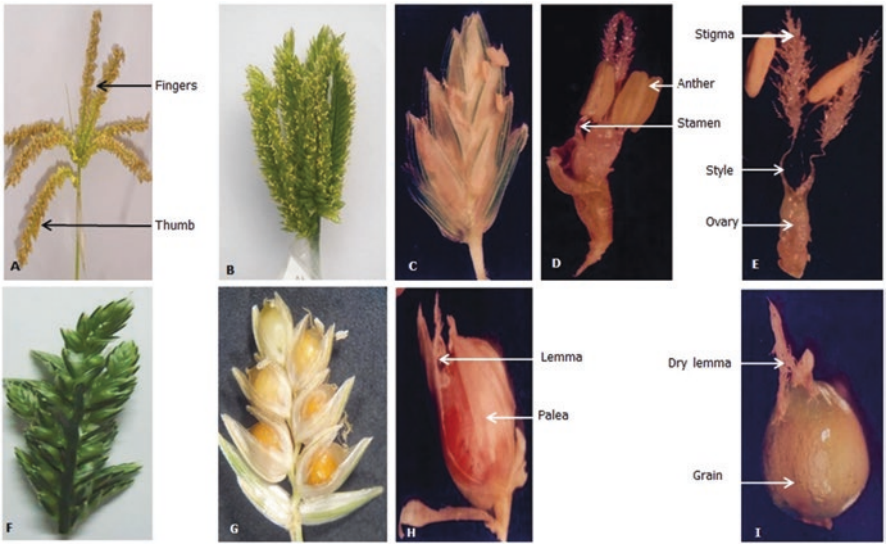

Fig. 3.5 Different parts of inflorescence in *Eleusine coracana* (L.) Gaertn. (**a**) Complete spike or inflorescence, (**b**) Inflorescence showing flowers on the edge of fingers, (**c**) Floret (spikelet), (**d**) Developing embryo in S1 stage, (**e**) Developing embryo in S2 stage, (**f**) Finger with developing grains in S3 stage, (**g**) Single spikelet with maturing grains in S4 stage, (**h**) Grain with dried lemma and palea still attached, (**i**) Developed grain with remnants of stigma and stamen attached at the top
Source: Mirza et al. (2014a)

lower known as a *thumb*, giving the inflorescence a bird-foot appearance (Fig. 3.5a). The complete emergence of the inflorescence may take up to 10 days. Each spikelet consists of 3–13 florets. Flowering takes place simultaneously in all fingers and begins from the top (Fig. 3.5b,c). Usually, flowering is complete by third day; however, it varies from place to place depending on temperature and humidity. The terminal floret is mostly sterile. Florets are hermaphroditic having boat-shaped lemma, a smaller palea with two lodicules (Fig. 3.5g, 6h). Before anthesis florets are compact, the androecium and gynoecium are very small, closely arranged and pale in color (Fig. 3.5d).

The androecium consist of 2–3 stamens with long filaments and short oblong anthers to form the ovary with 2 styles and a plumose stigma forms the gynoecium. After anthesis, the anthers and feathery stigma are visible at the tip of the florets (Fig. 3.5c); anthers, filaments, stigma and style increase in size, anthers appear yellowish due to pollen grains and the ovary is swollen (Fig. 3.5e). Pollen viability is very short in finger millet, only 10–15 min and the stigma is receptive for up to 5 h (Dodake and Dhonukshe 1998). Opening of the florets and grain filling starts from bottom to top within the spikelets (Fig. 3.5f). The nonshattering spikelets bear plump grains, usually enclosed in a thin brown pericarp that is exposed between the lemma and palea (Fig. 3.5g, 6h). Variation in head shapes and grain shapes helps to distinguish closely related species (De Wet et al. 1984).

3.4 Domestication, Selection and Early Improvements

Finger millet originated in the highlands of Uganda and Ethiopia and domestication began there around 5000 years ago, as evident from the archaeological records of early African agriculture (Hilu and de Wet 1976; FAO 1995; NRC 1996). Finger millet arrived in India probably more than 3000 years ago; India has been debated as its origin for a long time due to the presence of several cultivars in different regions. However, Fuller (2002, 2006) did an exhaustive review of the work on the origin of *Eleusine* and confirmed its African origin. Fuller reported that most of the claims of Indian origin of finger millet are widely based on misidentified material of other species. *Eleusine indica* is evidently the maternal diploid genome donor (AA genome) of both *E. coracana* subspecies resolved through various cytological, isozymes, RAPD, chloroplast DNA and genomic in situ hybridization (GISH) studies (Bisht and Mukai 2001a; Chennaveeraiah and Hiremath 1974; Hilu 1988, 1995; Hilu and de Wet 1976; Werth et al. 1994;). Using GISH, Bisht and Mukai (2001b) also suggested *E. floccifolia* as the B genome donor. However, Neves et al. (2005) rejected the assertion based on their nuclear internal transcribed spacers (ITS) and plasmid trnT-trnF sequence analysis. The sequence divergence and population structure analyses of 14 wild *E. coracana* ssp. *africana* lines and 79 cultivated finger millet accessions (*E. coracana* ssp. *coracana*) from African and Asian countries using SSR markers by Dida et al. (2008) supported the African origin of finger millet. They suggested that finger millet was first domesticated in the African

highlands, then moved to the southern lowlands, and finally was brought to India. The gene flow between the African wild and cultivated subpopulations indicate the natural hybridization among these sympatric subspecies. The B genome donor most likely has become extinct (Liu et al. 2014).

3.5 Germplasm Biodiversity and Conservation

3.5.1 Cytogenetic Analysis

The haploid chromosome number in the annual species of finger millet was reported first by Krishanswami and Ayyangar (1935) to be 9 in *Eleusine indica*, 18 in *E. coracana*, 18 in *E. brevifolia* Wall. and 17 in *E. aegyptica* (L.) Desf. Bisht and Mukai (2000) counted the diploid chromosome number in annuals as 36 in *E. coracana*, 18 in *E. indica* and *E. tristachya*, and 16 in *E. multiflora* while the perennials, *E. floccifolia* has 18, *E. intermedia* 18, and *E. jaegeri* 20 chromosomes. The DNA content in the leaves and roots was measured through laser flow (Mysore and Baird 1997). The 2C DNA content of *E. indica*, *E. tristachya*, *E. jaegeri*, *E. multiflora* and *E. floccifolia* ranged from 1.51–2.65 pg while that of the polyploid species *E. coracana* ssp. *coracana*, *E. coracana* ssp. *africana* ranged from 3.34–3.87 pg. In a series of fluorescent in situ hybridization (FISH) studies based on the hybridization of a 5sRNA probe of the chromosomes, Bishit and Mukai (2000, 2001a; b) reported that there were 3 diploid species, *E. indica, E. intermedia* and *E. floccifolia* and 2 tetraploids, *E. africana* and *E. coracana*. They also suggested that *E. multiflora* is a distinct species, the 2 tetraploids are related and that the 2 diploid species *E. indica* and *E. floccifolia* are probably the donors to the tetraploid species. This hypothesis was later refuted when the ITS (internal transcribed spacer) based phylogenetic analysis of species sequence data showed that *E. coracana* and *E. floccifolia* are not related (Neves et al. 2005). *Eleusine indica* was concluded as the progenitor of *E. coracana* ssp. *coracana* and *E. coracana* ssp. *africana* on the basis of the restriction analysis of chloroplast DNA (Hilu 1988). The RFLP data of Hilu and Johnson (1992) appeared to corroborate that *E. indica* is one of the parent species of finger millet. The RFLP and ISSR analysis by Salimath et al. (1995) and ITS based-phylogenetic analysis further helped in differentiating the species.

3.5.2 Germplasm and Genetic Diversity

For success in any breeding program and crop improvement effort, it is crucial to understand the amount and distribution of variability present in a gene pool. As finger millet is cultivated under diverse climatic conditions in Asia and Africa, understanding the genetic diversity is vital to identifying genotypes resilient to climate change (Mercer and Perales 2010). Genotypes tolerant to various biotic and

abiotic stresses have more allelic variation compared to susceptible types and thus are very useful for breeding programs. The DNA-based markers such as random amplified polymorphic DNA (RAPD), restriction fragment length polymorphism (RFLP), inter-simple sequence repeats (ISSR) and simple sequence repeats (SSR) have frequently been used for the analysis of genetic diversity in finger millet (Babu et al. 2014a; Bezaweletaw et al. 2011; Das and Misra 2010; Fakrudin et al. 2004; Gupta et al. 2010; Parani et al. 2001; Patil and Kale 2013). It is reported that large variation exists for agronomically- and nutritionally-important traits.

Barbeau and Hilu (1993) observed wide variations in the protein (7.5–11.7%), calcium (376–515 mg/100 g) and iron (3.7–6.8 mg/100 g) content in 2 wild and 8 domesticated cultivars. The wild cultivars were significantly higher in protein, calcium and iron than many domesticated accessions. The wild species were also found to be higher in the essential amino acids including lysine. Das et al. (2007) used RAPD markers to distinguish lines from Orissa from those originating from the southern states of India. Bezaweletaw (2007) analyzed over 64 landraces from Ethiopia and Eritrea and found great variation in several characters such as plant type, seed color, seed shape and persistence of pericarp. Plants with decumbent and prostrate types were found in Ethiopia, while erect types were found in the Eritrea collection. Srinivasachary et al. (2007) aligned the finger millet probes (332 loci detected by 266 probes or primer pairs) on a rice linkage map and compared 9 linkage areas and found duplication, deletion and sequence translocation. Dida et al. (2008) indicated that wild and cultivated accessions differed by a range of domestication-related characters, such as tiller number, plant height, peduncle length, seed color and grain yield. They also identified that the Asian and African subpopulations significantly differed in plant architecture and yield and the Indian alleles most likely contributed to the varietal enhancement. The genetic diversity and population structure were assessed in a number of Indian and non-Indian genotypes and collected from various geographical regions using 25 RAPD and 72 genomic SSR markers (Ramakrishnan et al. 2016a, b). Molecular variance and population structure in 42 genotypes of finger millet collected from different geographical regions of southern India were analyzed using 10 RAPD, 9 ISSR and 36 SSR markers (Rajendran et al. 2016).

Gimode et al. (2016) identified 10,327 SSRs and 23,285 nonhomologous SNPs from 2 cultivated finger millet genotypes KNE755 and KNE796. A number of markers of each type were analyzed across a diverse set of wild and cultivated finger millet germplasm for polymorphism. Polymorphism was shown by 95% (76 out of 80) of the SNP markers across 30 wild accessions while only 27.5% (22 out of 80) were polymorphic across the 59 cultivated genotypes revealing low variability within the cultivated finger millet. Most wild accessions were new collections that were expected to be cross- compatible with cultivated species, but the SNP markers clearly discriminated the wild species from cultivated ones and enabled correct classification of unknown genotypes. The analysis showed higher levels of homeologous SNPs which might suggest independent segregation of the AA and BB subgenomes. The recently released WGS will further help in SNP based diversity analysis in finger millet accessions.

3.5.3 Genetic Resource Conservation

For crop genetic improvement and subsequent utilization, conservation of the germplasm, evaluation and characterization of the existing diversity is vital. *Ex* situ conservation prevents the loss of genetic diversity and resources crop breeding programs. For ex situ conservation, seeds are preserved in national crop diversity collections, international genebanks such as those of the Consultative Group for International Agricultural Research (CGIAR), the Millennium Seed Bank, Royal Botanic Gardens Kew and the Svalbard Global Seed Vault (SGSV). SGSV holds 22,000 accessions of millets. Gene banks altogether hold more than 29,000 finger millet germplasms.

The International Crop Research Institute for the Semi-Arid Tropics (ICRISAT) Genebank is one of the largest international genebanks that serves as a world repository for the six mandate crops i.e. sorghum, pearl millet, chickpea, pigeonpea, groundnut, finger millet and five small millets with over 126,830 germplasm accessions collected from 144 countries. In addition, the ICRISAT Genebank has also deposited over 111,000 accessions at SGSV, Norway. ICRISAT currently has a collection of 7519 germplasms (http://genebank.icrisat.org/IND/Passport?Crop=Finger+millet) from several Asian and African countries. Most of the collection constitutes traditional cultivars and landraces (7121). The collection also includes 143 advanced or improved varieties 205 wild varieties and 50 accessions of breeding/research material. The Indian germplasm collection in general has early-maturing varieties combining high grain yield, quality and stover yield whereas African germplasm are said to possess higher level of resistance to blast (Babu et al. 2013a).

A core collection of 622 accessions was developed in 2004 from the entire global collection, 5940 accessions at that time, based on origin and data related to 14 quantitative traits (Upadhyaya et al. 2006). Later, the data of this core collection were evaluated for 20 morphological descriptors at 5 agro-ecologically diverse locations in India during the 2008 rainy season (Upadhyaya et al. 2010). The hierarchical clustering of data based on phenotypic distances resulted in 40 clusters and about 10% or a minimum of 1 accession was selected from each cluster to form a mini-core. The mini-core collection is comprised of 80 accessions. Two more gene banks in India at the National Bureau of Plant Genetic Resources (NBPGR), New Delhi and the National Active Germplasm Collection Site (NAGS) located at All India Coordinated Small Millets Improvement Project (AICSMIP), Bangalore have collections of 10,507 and 7070 accessions, respectively. Other institutes involved in finger millet research such as the Kenya Agricultural Research Institute (KARI) (2875), Institute of Biodiversity Conservation (IBC), Ethiopia (2156), Serere Agricultural and Animal Production Research Institute (SAARI), Uganda and the USDA Agricultural Research Service (USDA-ARS), United States (1452) also have reasonable collections of germplasm. The ARS-USDA in Griffin, Georgia, maintains 766 finger millet accessions from 11 countries (Ethiopia, India, Kenya, Nepal, Pakistan, South Africa, Tanzania, Uganda, Zaire, Zambia, Zimbabwe), of which 17

are wild relatives (*Eleusine floccifolia*, *E. indica*, *E. jaegeri*, *E. multiflora*, *E. tristachya*).

Genetic erosion of millets occurs mostly due to their underutilization, poor yield, and a policy shift that has focused on staple crops such as rice, corn and wheat or cultivation of only a small number of improved millet cultivars. Genetic erosion however, can also occur at the level of germplasm collections and genebanks due to inadequate management and regeneration failures. In situ conservation involves the rescue and maintenance of species in their natural environments, thus ensuring continued evolution in the field, including the natural exchange of genes with each other and their cultivated relatives. The Global Crop Diversity Trust, along with the Millennium Seed Bank, are working towards in situ conservation of 29 crops including finger millet, under the ten year project named Adapting Agriculture to Climate Change: Collecting, Protecting and Preparing Crop Wild Relatives (CWR). It is supported by the Norwegian government. Numerous partners all over the world (Fig. 3.6) are implementing the project, which supports CWR prioritization, collecting, conservation and pre-breeding.

Fig. 3.6 Crop Wild Relatives (CWRs) Project Map depicting the partner institutes involved in collection and conservation of finger millet CWRs across the globe **1.** Instituto de Investigaciones Agropecuarias (INIA), **2.** Embrapa Genetic Resources & Biotechnology **3**. Museu Nacional de Historia Natural e da Ciéncia, **4**. International Center for Agricultural Research in Dry Areas (ICARDA), **5**. Plant Genetic Resources Research Institute, **6**. National Centre for Genetic Resources and Biotechnology (NACGRAB), **7**. Plant Genetic Resources Centre (PGRC), **8**. Kenya Agricultural and Livestock Research Organisation (KALRO), **9.** Ethiopian Biodiversity Institute (EBI), **10**. Agricultural Plant Genetic Resources Conservation and Research Centre (APGRC), **11**. Plant Genetic Resources Institute (PGRI) and **12.** National Agriculture Genetic Resources Center Source: www.cwrdiversity.org

3.6 Cultivation Practices

Finger millet cultivation practices in different regions depend upon the climate, variety, soil type and water availability. It may be grown as a hot weather crop, from May to September, using long-duration cultivars and as a cold season crop, from November and December, using the early-maturing cultivars. Finger millet is cultivated under both irrigated and rainfed conditions. It requires only moderate rainfall and under a rainfed system, it is cultivated either as a direct sown crop or is transplanted. Under irrigated conditions, it is cultivated by direct sowing, transplanting or using a system of crop intensification (SCI) methods. The frequency of irrigation varies with the season. Finger millet is monocropped under irrigation or transplantation and intercropped under rainfed conditions. In India, the common crops grown in association with finger millet are lablab bean (*Lablab purpureus* (L.) Sweet), pigeon pea (*Cajanus cajan* (L.) Millsp.), cowpea (*Vigna sinensis* (L.) Walp.), and niger (*Guizotia abysinnica* (L.f.) Cass.). Finger millet is grown as the subsidiary crop with groundnut (*Arachis hypogaea* L.). In Nepal, it is grown as a relay crop, intercrop or mixed crop along with maize, wheat and barley under rainfed conditions (MoFSC 2002; Sharma 2001).

3.6.1 Crop Intensification (SCI)System

On the basis of practices and experiences with the system of rice intensification (SRI) (SRI International Network and Resources Center, Cornell University; http://sri.ciifad.cornell.edu), a system of crop intensification (SCI) has been developed in recent years in several Asian and African countries. SRI is based on a set of principles and practices for increasing the productivity of irrigated rice by changing the management of plants, soil, water and nutrients. SRI is not a fixed set of technical stipulations, but a system that mainly focuses on altering certain conventional agronomic practices with regard to four main components: soil fertility management, planting method, water (irrigation) management and weed control. However, the fundamental principles remain more or less the same. These four components are:

1. Development of healthy young plantlets for transplantation, avoiding any shock or trauma to the plant and taking care to conserve and nurture their potential for root system growth,
2. Significant reduction in crop density; keeping wider spacing between individual plants, giving them more room to grow both horizontally and vertically,
3. Avoiding synthetic fertilizers, pesticides and herbicides and enriching the soil with organic matter by using compost or farmyard manure,
4. Maintenance of proper soil aeration and water to avoid hypoxic conditions or flooding and to support better growth of plant roots and of beneficial soil microorganisms.

SCI management has now been widely applied to finger millet and is known as System of Ragi Intensification (SRI) or System of Finger Millet intensification (SFMI). SCI methods have demonstrated numerous benefits in finger millet cultivation and production. SRI practices lead to higher head recovery and increased grain and straw yield. It reduces the crop duration by about 10 days and reduces the number of chaffy grains. Under SRI practices, only 1.25 kg/ha was utilized as compared to 3–5 kg/ha employed in conventional methods. It also improved cold tolerance in plants.

India In India, conventional cropping by broadcasting finger millet seed on a tilled field, yields 1.25–2 mt/ha and up to 3.75 mt/ha with good irrigation and fertilizers. However, with SRI-like practices developed by the farmers at Haveri, Karnataka, known as the *guli vidhana* (pit system) methodology, yields increased to 3.75–6.25 mt/ha. Farmers transplant 12-day-old seedlings in shallow furrows at wide spacing. Between 15–45 days after transplanting, a light board is pulled over the plants in the field in different directions. The bending causes moderate stress leading to growth of new roots and tillers from the crown meristematic tissue. It also loosens the soil, increasing aeration and cuts the roots of young weeds. A similar practices called the System of Finger Millet Intensification (SFMI) developed by farmers with the help of the NGO PRADHAN (2012) in the eastern state of Jharkhand, yields increased in their rainfed crop from 1 mt/ha to ≥3 mt/ha. The People's Science Institute (PSI) introduced these practices in the Himalayan state of Uttarakhand leading to a 60% increase in grain yield. SCI practices increased the yield from an average of 1.5 to 2.4 mt/ha.

Africa Farmers started practicing these methods in Tigray, Ethiopia in 2003, call it *planting with space* (Araya et al. 2013). The yield in finger millet increased to 3.5–7.8 mt/ha from 1.4 mt/ha in fields established by broadcasting and 2.8 mt/ha with liberal use of compost. Farmers are also implementing these methods in other crops.

3.6.2 SRI/SCI Constraints

SRI is labor intensive and requires certain skill levels. Planting and weeding are initially the most labor intensive parts of SRI. Hence, farmers are hesitant to adopt it due to higher cost and risk, especially for large-scale production. It is difficult to monitor water levels and avoid flooding in the rainy season due to unpredictable weather. However, the labor and cost is reduced over time. While SCI initially increased cost of production by about 25%, the higher yields reduce their costs of production by 60%. Proper training and knowledge of the benefits and availability of low-cost tools will encourage the farmers to adopt these practices.

3.7 Current Agricultural Challenges

Finger millet production is affected by both biotic and abiotic stresses. Also, various fungal and bacterial diseases and pests cause considerable damage to the crop.

3.7.1 Biotic Constraints

Insect pests and diseases are the greatest challenge to agriculture and food security. There are at least 120 insect pest species recorded on finger millet in Asia and Africa. Table 3.2 lists the major biotic constraints affecting finger millet production worldwide.

3.7.2 Abiotic Constraints

In semiarid and arid regions, low and erratic rainfall and periodic drought are major abiotic stresses affecting crop productivity. Drought intensity and frequency has increased in the recent past accompanied by serious reductions in rainfed agricultural outputs. Global warming and changing climate will only exacerbate the conditions especially in these regions by reducing the grassland productivity by 49–90% by 2020 (UN 2011). A 10% decline in the level of rainfall in Ethiopia resulted in an average drop of 4.2% in cereal yields (Webb and Braun 1994). A study on finger millet landraces in which a drought treatment was imposed 4 weeks after sowing resulted in 100% yield loss and over 30% loss in biomass (Maqsood and Ali 2007). As much as half of the world's irrigated lands and more than 20% of its cultivated area are affected by salinity (Rhoades and Loveday 1990). The osmotic potential of soil solution decreases at high salt concentrations creating water stress in plants and finally causing ion toxicity. Finger millet is generally grown in marginal areas with low soil fertility and nutrient stresses, especially in Sri Lanka and African countries. In future, the N and P demands may also affect the production of finger millet in low-input agricultural systems of Asia and Africa since the crop is largely grown by resource-poor farmers who cannot afford to buy expensive fertilizers (Thilakarathna and Raizada 2015). In addition to these abiotic constraints, harvesting and postharvest handling is still a labor intensive practice in several finger millet growing countries.

Table 3.2 Major finger millet pests and diseases

Pest/Pathogen	Symptoms	References
Pink stem borer (*Sesamia inferns*)	Larvae eat central leaves causing "pin holes", bore into stems and shoots causing empty panicles (white ears)	Baladhiya et al (2018), Sasma (2018), www.agritech.tnau.ac.in, www.aicrpsm.res.in, http://cropgenebank.sgrp.cgiar.org
White borer (*Saluria inficita*)	Larvae bore into the stem at the base close to the soil level and cause "dead heart"	www.agritech.tnau.ac.in, www.aicrpsm.res.in
Ear head caterpillar (*Euproctis subnotata*)	Adults infest the inflorescence at the milky stage turning spikes chaffy and covered with silky webs	Kalaisekar et al. (2017), www.agritech.tnau.ac.in
Brown aphid (*Hysteroneura setariae*)	Aphid feeding causes yellowing of leaves, severe infestation covers whole plant and causes stunted growth	Kalaisekar et al. (2017), www.agritech.tnau.ac.in, www.aicrpsm.res.in, http://cropgenebank.sgrp.cgiar.org
Root aphid (*Tetraneura nigriabdominalis*)	Aphids feed externally on the sap, plants turn pale, stunted, wilted and finally dry up	Gadiyappanavar and ChannaBasavanna (1973), www.agritech.tnau.ac.in, www.aicrpsm.res.in, www.plantwise.org
White grub (*Phyllophaga* sp.)	Feeds externally on the roots, inflorescence and leaves, causing wilting and finally death in seedlings and young plants; reduced vigor and loss in grain yield in large plants	www.plantwise.org, www.aicrpsm.res.in, http://cropgenebank.sgrp.cgiar.org
Root grub (*Holotrichia consanguinea*)		
Defoliators	Defoliating insect pests damage plants by eating away the leaves. They feed on the green matter leaving only the veins. A substantial loss of photosynthetic tissue leads to critical damage to the plant growth, increased susceptibility to attack by other insects and pathogens and even plant death	Kalaisekar et al. (2017), www.aicrpsm.res.in, www.agritech.tnau.ac.in
Cut worm (*Spodoptera exigua* Hübner) Armyworms (*Spodoptera* sp.)		
Black hairy caterpillar (*Estigmene lactinea*)		
Leaf folder (*Cnaphalocrocis medinalis*)	Larvae fold a leaf blade together with its silk strands, feeds inside creating longitudinal white patches and transparent streaks	Murthy et al. (2015), Kalaisekar et al. (2017), www.plantwise.org, www.aicrpsm.res.in, www.cabi.org
Grasshopper (*Chrotogonus trachypterus*)	Nymphs and adults feed by marginal notching of the leaves. In case of severe infestation, they defoliate entire leaves and graze over the entire field	www.agritech.tnau.ac.in
Leaf hoppers/Ragi Jassid (*Cicadulina* sp.)	Suck the plant sap causing withering and drying	Kalaisekar et al. (2017), www.aicrpsm.res.in, www.agritech.tnau.ac.in

(continued)

Table 3.2 (continued)

Pest/Pathogen	Symptoms	References
Blast *(Magnaporthe oryza)*	Causes blast in young leaves; also affects neck, spike; small brown circular to elongated spots on leaves elongate to spindle-shaped areas, coalesce and cause drying of foliage; conidia produced at the center give spots a smoky appearance; neck region turns black and shrinks obstructing grain formation, partially or completely reducing spikelet length, grain number, grain weight; infected seeds show reduced germination	Rath and Mishra (1975), Ekwamu (1991), Nagaraja et al. (2007), Singh and Kumar (2010), Kumar and Kumar (2011), Babu et al. (2013b), Klaubauf et al. (2014) and Gashaw et al. 2014
Blight (*Helminthosporium nodulosum*)	Causes seed blight; can infect all plant parts, throughout the life cycle; several minute, oval, light-brown lesions on the young leaves coalesce to form large dark brown patches killing the seedlings prematurely; in mature plants, it causes linear oblong and dark brown spots on the leaves, prominent brown to dark brown discoloration in neck region leading to heavy chaffiness, breakage of head; secondary infection can occur through air borne conidia	Kalaisekar et al. (2017), www.aicrpsm.res.in, www.agritech.tnau.ac.in
Sclerotium rolfsii Sacc.	Causes foot rot or wilt on the basal region of stem, causing large dark brown lesions and become soft; small, spherical, dark-colored sclerotia appear on the surface of the lesions; hindered transport of water and nutrients ultimately causes plant death. The plants become stunted	Nagaraja et al. (2007), www.aicrpsm.res.in
Pseudomonas syringae pv. *syringae*	Causes bacterial brown spot; small, water-soaked lemon yellow spots that enlarge, coalesce, turn brown and become necrotic; often light-cream or silver exudates are produced on the lesions under moist conditions	Nagaraja et al. (2007), www.aicrpsm.res.in

(continued)

Table 3.2 (continued)

Pest/Pathogen	Symptoms	References
Xanthomonas sp.	Causes leaf streak disease; narrow, water-soaked, transparent lesions on leaves that turn red, opaque and coalesce to form long irregular streaks and blotches extending across the leaf blade, characterized by dead tissue bordered by narrow, dark margins; light-yellow exudate dries to form thin white or cream scales; infected plant debris also transmits the bacteria	Nagaraja et al. (2007), http://cropgenebank.sgrp.cgiar.org, www.aicrpsm.res.in

3.8 Traditional Breeding Methodologies and Limitations

Plant breeding is cultivar development, crop improvement and seed improvement of various agriculturally- and horticulturally-important crops, conventionally by selective mating or hybridization. Early finger millet breeding was largely confined to India, particularly in the southern states of Tamil Nadu, Karnataka and Andhra Pradesh. Later, it spread to other Indian states such as Maharashtra, Gujarat, Orissa, Bihar and Uttarakhand. The East African countries involved in finger millet breeding include Uganda, Zaire, Malawi and Zimbabwe. Finger millet breeding is also reported from Sri Lanka, Malaysia and the Philippines. In the European colonial period, indigenous crops were largely ignored. Yield levels were very low due to lack of inputs, poor soil fertility, rainfed farming, low-yielding cultivars and lack of improved agronomic practices. Initial breeding efforts in finger millet were limited due to its self-pollinating nature. Development of emasculation and pollination techniques created the opportunity to improve the crop and create new hybrids. Later, various breeding approaches such as pure-line selection, recombination breeding and mutation breeding were extensively used for the genetic improvement of finger millet. The breeding strategies for selection and genetic improvement have greatly improved since the availability of genomic data and genome editing tools.

3.8.1 Pure-Line Selection

The earliest reports of finger millet improvement are from India, where crop improvement was initiated by Leslie C. Coleman, the second director of agriculture of Mysore State in Karnataka. He initiated the work on pure-line selections from indigenous cultivars such as Hullubele, Gidda and others in 1913 at the Zonal Agricultural Research Station, V.C. Farm, Mandya and Hebbal farms, Bangalore. He contributed the first finger millet cv. H-22 in 1918 and his concerted efforts resulted in the release of several other cvs. such as K-1, R0870, ES-11, ES-13 CO-1

and H-1. For pure-line selection, single superior plants are selected from a population and the superior progeny selected on the basis of characteristics such as superior spikes, high yield, earliness, and pest and disease resistance. Any progeny superior to an existing cultivar is then released as a new pure-line cultivar. The line can be tested in multiple locations and released. Pure-line selection resulted in the development and release of several other cultivars of finger millet in India such as CO-2, CO-3, CO-7, CO-8, PLR-1, K-22, ES-11, RO-786, AKP6, VZM2 and Aruna. Three improved pure lines D-11 (early), D-31 (mid-late) and A-16 (late) were released at Hathkamba, Konkan in 1921.

In Africa, selection and preservation of superior heads from indigenous cultivars formed the basis of seed for the subsequent season and a major step toward crop improvement (Jameson 1970; Khizzah 1985). Research work on finger millet improvement began with the initiation of a millet breeding program at Serere Research Station, Uganda, and to a limited extent in Tanzania, Malawi and Zambia (Peters et al. 1967–1971). Several high-yielding cultivars were identified including Phagalala and Fumbat (Nyasaland-AQ 1951) from Malawi; Vuri, Lango and Omidu from Zaire (INEAC 1956, 1958); Kiyaka and the Kisozi from Rwanda, Burundi; Kiega and 1-M strains of Mphunsi and 0–9 and B.K. strains of Agahagarika (Bruyere 1958) from Zaire and Gulu E and Serere-1 from Uganda (Peters et al. 1970). Later, Engeny, P283, WC65 and P224 (PESE1) cvs. were introduced (Zake and Khizzah 1986). In Ethiopia, KNE 409, KNE 1098, Acc 100057 and KNE 479 (Mulatu et al. 1985) and in Kenya, Gulu E, P224, KA2 and KATFM1 were identified as high-yielding cultivars (KARI 1990).

Although the early efforts largely focused on the development of pure breeding strains and cultivars, Ayyangar (1932) proposed the development and improvement of composite cultivars. He proposed that this would help in developing cultivars with hybrid vigor and a much greater range of adaptation to erratic weather due to the natural crosses among the different genotypes. This paved the way for hybridization techniques for finger millet improvement.

3.8.2 Hybridization Breeding

Finger millet genetic improvement got a boost after the establishment of hybridization techniques and several new cultivars were released. The aim of hybridization is to combine desirable genes found in two or more different plants or cultivars and to produce pure-breeding progeny superior to the parents.

3.8.2.1 Hybridization Techniques

Contact Method Successful hybridization in finger millet was achieved through the contact method (Ayyangar 1934) in the 1950s. Ayyangar suggested the exploitation of dominant characters in the male parent. This method involves

removal of all except a single ear or finger in the desired plants and the panicles of the selected parent plants are tied together before flowering, to enhance the chances of natural cross-pollination. The two panicles are enclosed in a bag to prevent unwanted pollen. This results in low frequency of true hybrids, which can be identified with the help of dominant characteristics of the parents as a marker in the F1 generation such as pigmentation in the nodes of male parent (Gupta 2006). The results obtained with contact method were generally inconsistent.

Hot Water Treatment Emasculation is essential for successful hybridization in self-pollinated plants. Manual removal of the immature anthers using forceps or needles is very difficult in finger millet due to the small size of the florets. As an alternative, Rao and Rao (1962) suggested the hot water treatment for emasculation where the florets which are likely to flower in the next few (2–3) days are immersed in hot water. They emasculated the ears by immersion in water at 47 °C for 10 min, or at 48 °C for 7 min. This treatment did not damage other floral parts. Furthermore, Raj et al. (1964) found a hot treatment at 52 °C for 5 min quite successful. However, the procedure requires standardization depending on temperature and climatic conditions. These techniques have limitations in small millets probably as the delicate pistils are largely protected by glumes (Riley et al. 1989). Also, a combination of hot water and contact pollination was used which proved effective in obtaining reasonable quantities of crossed seeds.

Cold Water and Plastic Bag Method Later, a technique was developed at the University of Agriculture Sciences, Mandya, Bangalore, under the All India Coordinated Small Millets Improvement Project, to use cold temperature and humidity to induce flower opening. The fingers are sprayed with cold water and covered tightly with a polythene bag. The high humidity created in the plastic bag prevents anther dehiscence and anthers emerge without shedding the pollen (House 1985). The glumes slowly open and the premature anthers are exposed and thereafter removed carefully without injuring the stigma. The emasculated fingers are again sprinkled with cold water to prevent drying of the pistil.

3.8.2.2 Hybrid Cultivars

Using hybridization, four high-yielding cultivars were developed in India: Poorna (Co-1 x Aruna), Udaya (K-1 x Aruna), Annapurna (K-1 x Aruna) and Cauvery (Hulluble x H22). These cultivars showed up to 50% increase in yield potential and met to the needs of different finger millet growing seasons for a long time. Two more cultivars were developed through crossing, namely Shakti (Ro 013 x H22) and 5–6 (Co-1 x H22).

The development of high-yielding, white-grained finger millet also started in India at Coimbatore, Tamil Nadu (Wariar and Divakaran 1956). The first improved cv. E.C. 4310 was created by a cross between E.C. 1540 (low-yielding, white-grained strain, high vitamin-13 content) with male parent E.C. 985 (high-yielding,

brown-grained). A coordinated finger millet improvement program was initiated in India in 1963 to evaluate, screen and catalogue the 947 stocks of world collections.

The contributions of Indian breeder C.H. Lakshmanaiah to finger millet crop improvement are unparalleled. At the VC Farm, Mandya, Karnataka in 1964 he created new recombinant cultivars by crossing Indian cultivars with African ecotypes. A few African donor parents such as IE-927, IE-929, IE-980, IR-810 and IE-902 were identified by screening the available world collection of germplasm over 8 years. He crossed these lines with the local cvs. such as Hallubele, K1, Annapurna, Purna, Cauvery, Shakti, Co-1 and Hamsa. The hybridization resulted in 16 Indo-African cultivars with substantially more yield potential and these were designated as "Indaf" cultivars. These can be grown under both irrigated and rainfed conditions (Bhat et al. 2018; Lakshmanaiah 1967; Madhusudan et al. 2015; Zake and Khizzah 1986).

3.8.2.3 Male Sterility Breeding

Male sterility can effectively be achieved through male gametocides, chemical hybridizing agents such as maleic hydrazide, gibberellic acid (GA), ethyl methane sulfonate (EMS), ethrel, and physical agents such as fast neutrons. Hot water treatment of inflorescences at 52 °C for 5 min was found effective in inducing male sterility in finger millet (Raj et al. 1964). Male-sterile mutants in cv. Gulu E were created using fast neutrons at the Serere region under the East African Agriculture and Forestry Research Organization, Uganda (Mukuru et al. 1974).

A GMS line, INFM 95001, was developed for the male sterility locus ms1 using EMS (1.5% aqueous solution, for 6 h at 25 °C) jointly by ICRISAT and the Department of Agronomy, University of Nebraska, USA (Gupta et al. 1997). INFM 95001 is a white finger millet and is a medium maturity (94 days) cultivar. It was recommended in composite breeding and heterosis studies. A male-sterile plant is easily distinguished from a male-fertile plant at anthesis. As compared to using chemical hybridizing agents and cytoplasmic male sterility, nuclear-encoded recessive male steriles (ms) offer major advantages for hybrid breeding.

3.8.3 Mutation Breeding

Mutation breeding has been around since the 1930s. It is a powerful means of creating useful genetic variability. Mutation breeding simply accelerates the process of mutation in plant genetic material which otherwise is underway in nature. Mutation breeding is based on selfing of mutants instead of crossing as in conventional breeding, until the induced character has a stable expression in the subsequent mutant generations. It is cost effective, quick, robust, transferrable and ubiquitously applicable. There are more than 3200 mutant cultivars of more than 210 plant species from over 70 countries, including 2 cultivars of finger millet (FMM165, FMM175)

from Zambia, registered in the FAO/IAEA Mutant Varieties Database (https://mvd.iaea.org/) and released for commercial use. The most common method of mutation breeding is to treat seeds with physical, chemical or a combination of both mutagens and selecting from the subsequent population the desirable mutants which are superior to their parents.

Mutation breeding in finger millet started in southern India when Krishnaswami and Ayyangar (1941) irradiated seeds with X-rays. Cultivar Hagari-1, released in 1941, was the first successful mutant cultivar of finger millet developed using X-ray irradiation. Later three more cvs. CO-3 (1942, dwarf), Dibyasinha (1976, early maturing) and K-6 (1982, dwarf and early maturing) were released for commercial use. Goud et al. (1969, 1971) studied the effects of gamma irradiation and EMS on cvs. Purna and Hamsa and several viable mutations of potential breeding value were produced in the cv. Purna. Sinha and Sahoo (1971) developed three early-maturing mutant lines by treated seeds of finger millet cv. AKP-7 with chemical mutagens ethyl methane sulfonate (EMS) and nitroso guanidine (NG). Among these, the early maturing (90 days) cv. Dibyasinha was released for commercial use. Another promising mutant M21 of cv. HES 927 was created using gamma irradiation of the seeds (Shivashankar et al. 1973). This mutant was high yielding and blast resistant. Nayar et al. (1974, 1979) treated different cultivars of finger millet with gamma-rays, fast neutrons and EMS. Mutants (fast neutrons) for ear shape and type namely, semi-compact, open and lax were isolated for cv. Hamsa which otherwise has very compact and fist-like ears, thus harbors many insect pest and diseases. Tikka (1985) isolated a number of dwarf and early-maturing mutants of six cultivars of finger millet (PR 202, Co10, Indaf-9, HR 24, IE 744, GN_1) by treating the seeds with physical (gamma-rays) and chemical mutagens such as EMS, methyl methane sulfonate (MMS) and diethyl sulfate (DES). High-yielding mutants of white finger millet cv. Co 9 were obtained with low doses of EMS and NG (Devkota 1987), short-duration mutants were obtained for cv. Sarada and bold grain mutants for MS2698 with NG (Raveendran et al. 1982). Devkota (1987) also suggested that there was scope for improvement through a second cycle of mutagenic treatment. Several dwarfs, early types and high tillering type mutants were developed from PR 202, HR-911, Indaf-8 and TNAU-294 cvs. Using gamma-rays (Gowda and Seetharam 1983).

Sreekantaradhya (1979) estimated the LD_{50} dose of gamma-rays and EMS in finger millet. Mahishi and Seetharam (1983) concluded that lower doses of gamma-rays and chemical mutagens EMS, MMS, nitroso methyl urea and 1-methyl-3-nitro-l-nitrosoguanidine are more effective. Gamma-rays, X-rays, EMS and DES have been widely used since for developing mutant lines. Several studies support these findings and for further calibrating the dosages for different mutagens. More recently, Eswari et al. (2014) identified desirable mutants for plant height, tillers/plant, productive tillers, finger number, finger length and 1000-grain weight for cv. TRY 1, and suggested a dosage of 0.15% of EMS to be ideal. Mutant cvs. FMM165 and FMM175, currently registered in the FAO/IAEA Mutant Variety Database (https://mvd.iaea.org), were developed using X-ray irradiation at the Zambia

Agriculture Research Institute (ZARI). They were isolated for increased finger length and number of fingers.

In many instances the alternate alleles e.g. resistant and susceptible gene vary by only a few bases (Bryan et al. 2000). Gene editing technology (GenEd) can be used to mutate the susceptible alleles to resistance directly rather than by a series of crosses and backcrosses (Georges and Ray 2017). Mutants can also be developed in polyploid plants using the CRISPR/CAS9 GenEd where mutants are often difficult to isolate, particularly in recent polyploids where all homeologues of a gene may be expressed (Georges and Ray 2017).

3.8.4 Improved Cultivars

Several coordinated projects have been undertaken recently by major international and national research institutions in India, African countries, Nepal and Sri Lanka by ICAR, KALRO, NaSARRI, EIAR, ICRISAT and ICARDA, to develop new improved cultivars of finger millet. Currently 143 advanced/improved cultivars are registered at ICRISAT.

3.8.4.1 India

Between 1986 and 1999 in India, the main focus was on developing cultivars with high grain and straw yield, as well as drought and disease resistance. Several hybrids as well as pure-line high-yielding cultivars (1500–5000 kg/ha) such as MR-2; MR-6; Indaf-15; VL124; HR911 (UAS 1 x IE 927); L-5 (Malawi x Indaf 9); Gautami (PR 1158–9) (PR 202 x U22) and Gujarat nagli 2 (NS 109) (Pureline selection) were released from different research centers. Blast-resistant cvs. GPU 28, Indaf 5 (Indaf 9 x IE 1012) and KM 65 and two drought tolerant cvs. RAU 8 (BR 407 x Ranchi Local) GN 3 (KM 13 x GN 2) were released. Two cultivars, a pureline Suraj (VR 520) and a hybrid Saptagiri (or PR 2614) (MR 1 x Kalyani), were developed in Andhra Pradesh with both blast and drought tolerance. Another cultivar, PR 230 (or Maruthi) with both blast and blight resistance was developed through pure-line selection at ANGRAU, Paleru, A.P. A salinity tolerant cultivar, TRY 1, was developed at TNAU, Coimbatore.

In the period 2000–2018, with the establishment of the AICRP on small millets, emphasis was on developing hybrid cultivars involving productive lines with elite backgrounds. Both early-maturing and long-duration cultivars with high yield potential and suitable for irrigated or rainfed conditions were released. Most of the cultivars were resistant to blast (neck and finger) disease. Numerous blast resistant cultivars of *GPU* and *KMR* series i.e. GPU-26, GPU-28, GPU-45, GPU-48, GPU-66, KMR-204, KMR-301 and KMR-340, with average yields of 2000–4000 kg/ha were released by AICRP (1986–2018) (Appendix II). A semi-dwarf, non-lodging cv. GPU-67 was also released which is suitable for cultivation in all finger millet

growing regions. Breeders also focused on tolerance to brown spot disease, stem borers and aphids. A somaclonal cv. Dapoli-2 (SCN-6) was developed through tissue culture at Dr. BSKKV, Dapoli, Maharashtra and released in 2017. The parent cv. Dapoli-1 (1985) was mid-late (125–135 days), non-lodging and responsive to nitrogenous fertilizers and with reddish brown grain color. The somaclone Dapoli-2 is a high-yielding cultivar rich in iron and calcium, moderately resistant to blast and tolerant to aphids and tobacco cutworm (*Spodopter littura*).

3.8.4.2 Africa

In Africa, a systematic regional finger millet program was initiated in 1985 by SADCC/ICRISAT (Southern African Development Coordination Conference) and ICRISAT (Gupta et al. 1986a, b). During 1985–1986, the program evaluated a total of 394 accessions collected from Zimbabwe (374), Zambia (14), Malawi (4) and Tanzania (2), to be used in crossing for hybrid development. From this program a new non-lodging cv. Steadfast was created by crossing the local lodging susceptible cv. M144 with Line 197. The local finger millet cultivars gave an average yield of 1600 kg/ha. With the establishment of regional cereal programs and concerted efforts of different centers, several high yielding improved finger millet cultivars such as Engeny, Gulu E, Serere 1, Pese 1, Seremi 1, Seremi 2, Seremi 3, SX 8, SEC 915 and SEC 934 were released over the years (Alimu 1985). These cultivars are also blast resistance, have good grain quality and early maturing (mostly within 90 days).

In 1993 two lines, KNE#1098 and KNE# 409, were identified as better yielding out of the 57 lines introduced by the East African Regional Sorghum and Millets Network (EARSAM), now renamed the East and Central African Sorghum and Millets Network (ECARSAM), across the intermediate to high elevation areas in Ethiopia. These lines were later released for commercial production in 1998 and named Tadesse and Padet, respectively. Due to severe drought in 2002, almost all crops in the dry districts of Ethiopia failed except finger millet cv. Tadesse (KNE# 1098). Another line, KNE# 411 was identified and released with the name Boneya by the Bako Agricultural Research Center in the western Ethiopian region in 2002. In Zimbabwe, a new high-yielding cv., SDEV 87001, was developed (Gupta and Mushoga 1994), which yields up to 3500 kg/ha.

The Kenya Agricultural Research Institute (KARI) developed new superior finger millet cvs. U-15, Gulu and Okahale-1 in 2011 that guaranteed higher yields. The cultivars are also tolerance to drought, striga weed and blast disease. Two more cultivars, a red-seeded Katumani and a brown-seeded P224, have been released recently. Katumani is a dwarf cultivar and is drought tolerant. It matures in 3 months and gives an yield of 700–1000 kg/ha. Cultivar P224 is tall, however, tolerant to lodging and blast. P224 matures in 3–4 months and yields 1000–1500 kg/ha of grain. With the help of ICRISAT and the Harnessing Opportunity Productivity Enhancement (Hope) Foundation, these new cultivars are being introduced in different provinces all over Africa.

3.8.4.3 Finger Millet Improvement in Other Countries

Nepal In Nepal, five varieties have been released by the Hill Crops Research Programme (HCRP), Kabre; Climate Change, Agriculture and Food Security (CCAFS) and CGIAR Center, for cultivation by local farmers (Table 3.3). Three of these cultivars originated in India. All the cultivars are non-lodging, drought tolerant and resistant to *Cercospora* leaf spot and blast diseases, except cv. Dalle-1.

Ukraine A somaclonal cv. Yaroslav-8 is listed in *Register of Plant Varieties Suitable for Dissemination in Ukraine* (Radchuk et al. 2012). It was obtained from the genetically-stable somaclonal variant line SE7 created by Bayer et al. (2007). The cultivar has several agronomically-important features, such as the most reduced plant height, high grain yield and green biomass, rapid germination at low temperatures and reduction in duration.

3.8.5 Interspecific Hybridization

Wild relatives of cultivated crops serve as a gene pool that could potentially be used to improve them. But to date, only cultivated species of *Eleusine coracana* have been used; there are almost no reports of using their wild relatives for crop

Table 3.3 Improved varieties released in Nepal

Variety	Pedigree	Institute where developed	Year of release	Av. yield (kg/ha)	Special features
Dalle-1 (IE-980)	Unknown	Origin-India; maintained at- HCRP, Kabre	1980	3300	Drought tolerant; non-lodging; susceptible to blast and *Cercospora*
Okhle-1 (NE1304-43)	Selected from local cultivar of Okhaldhunga	HCRP, Kabre	1980	3300	Drought tolerant; non-lodging; resistant to finger and neck blast, *Cercospora* leaf spot
Kabre Kodo-1 (NF-6401-26)	Selected from local cultivar of Surkhet	HCRP, Kabre	1990	1800–4800	Drought tolerant; non-lodging; resistant to finger and neck blast, *Cercospora* leaf spot
Kabre Kodo-2 (GE-5176)	Unknown	SAARC-RVT, India	2015	2530	Drought tolerant; non-lodging; resistant to finger and neck blast, *Cercospora* leaf spot
Sailung Kodo-1 (GE-5016)	Unknown	SAARC- RVT, India	2015	2490	Non lodging; moderately resistant to finger and neck blast, *Cercospora* leaf spot

Source: Joshi et al. (2017)

improvement. This may be due to availability of vast genotype variability in cultivated species, being robust and having higher grain quality then the wild types. Recently, Akech et al. (2016) identified blast-resistant lines from interspecific crosses between the wild (*E. kigeziensis* and *E. africana*) and cultivated types. From the F4 generation of crosses *E. kigeziensis* x Pese 1, *E. africana* x Seremi 1 and *E. africana* x Seremi 3; two lines resistant to all three forms of blast diseases were identified. They found 13 lines resistant to neck and head blast and moderately resistant to leaf blast. They also identified six lines were resistant to neck and head blast but susceptible to leaf blast. In view of the continual climate change and the need for germplasm suited to extreme environmental conditions, the necessity to conserve finger millet wild relatives for future breeding research cannot be ignored.

3.9 Role of Biotechnology

Conventional plant breeding is tedious, time consuming and affected by environment conditions that cannot be controlled. Nonetheless, biotechnological or molecular techniques such as genetic engineering and genome editing provide powerful tools for genetic manipulation of crops and speed up the process of crop improvement. In order to utilize these techniques, the inception of efficient in vitro regeneration systems for the transformation and regeneration of cereals is a vital prerequisite (Shrawat and Lörz 2006; Yemets et al. 2013). The earliest attempts at callus initiation and regenerating finger millet through tissue culture was made by Rangan (1976) and Mohanty et al. (1985) using leaf-base segments. Eapen and George (1990) utilized different explants such as shoot tips, leaf sheath fragments and undeveloped inflorescences for somatic embryogenesis. Since then, different plant tissues have been used as explants such as leaf sheaths, root mesocotyls, embryogenic seed, and mature and immature embryos (Ceasar et al. 2018). Shoot apexes have proved to be an efficient explant owing to its easy availability, accessibility, ease in handling and rapid regeneration of multiple shoots (Arockiasamy and Ignacimuthu 2007; Ceasar and Ignacimuthu 2008; Dey et al. 2012). Recently, Ngetich et al. (2018) reported an efficient protocol for somatic embryogenesis and plant regeneration in six African finger millet cultivars using shoot tips from 3-day-old in vitro grown plants and achieved a 97% survival rate.

Research on finger millet transformation was initiated by Gupta et al. (2001) using the biolistic method to compare the efficiency of five gene promoters on the expression of the β-glucuronidase (GUS) reporter gene. Latha et al. (2005) utilized the biolistics method to develop transgenic plants with resistance to leaf blast disease, which was further optimized by Jagga-Chugh et al. (2012). Several reports followed on attempting and optimizing protocols for *Agrobacterium tumefaciens*-mediated genetic transformation of finger millet. Ceasar and Ignacimuthu (2011) and Sharma et al. (2011) optimized *Agrobacterium*-mediated transformation using shoot apex and embryogenic seed. The desired gene is cloned in a binary vector and introduced into *Agrobacterium*. This recombinant *Agrobacterium* is co-cultivated

with the explants. The bacteria infect the plant cells and the gene of interest along with a suitable selectable marker is integrated into the plant genome. A mature plant regenerated from these transformed cells will contain the cloned gene in every cell and will pass the cloned gene to its progeny.

Direct plant organogenesis is also an effective method to produce multiple shoots with reduced somaclonal variations. It minimizes the culture duration and mutations by omitting callus formation and reducing sub-culturing cycles (Satish et al. 2015). Further optimization of the transformation technique using direct-plant regeneration was reported by Satish et al. (2017) (Fig. 3.7).

Recently, a regeneration system via direct organogenesis was reported using in vitro-derived shoot apical meristems (Mukami et al. 2018). The highest shoot induction was observed in MS medium supplemented with 1.75 mg/l benzylaminopurine (BAP). Yemets et al. (2013) reported an advanced and rapid method of plant regeneration through callus cultures of *Eleusine coracana* seeds. White nodulated calli were formed on medium with N6 macro-salts, MS micro-salts 2, 4-D (2 mg L^{-1}), kinetin (0.4 mg L^{-1}), NAA (2 mg L^{-1}) and certain additives (Fig. 3.8). They found NAA beneficial in view of callus regeneration capacity,

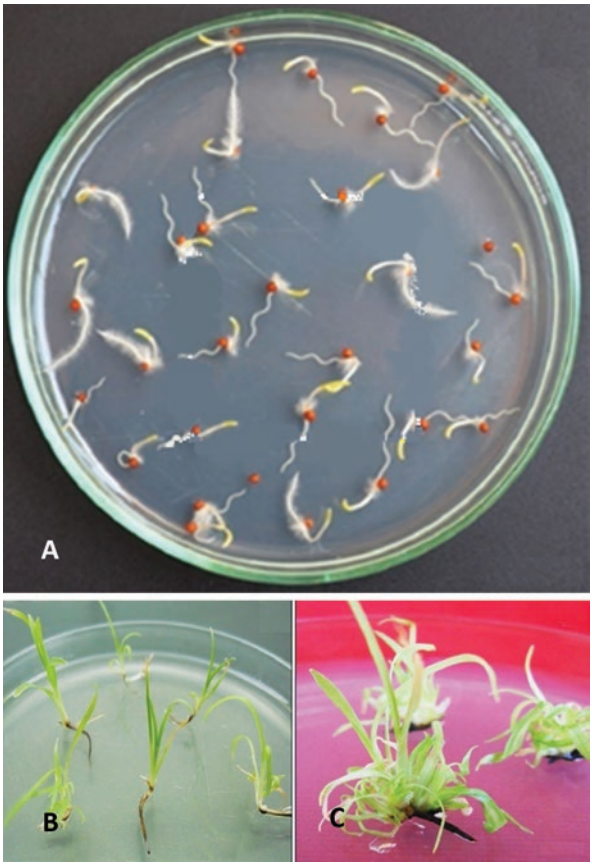

Fig. 3.7 Typical in vitro shoot apical meristems (SAM) explant preparation and direct shoot regeneration from a finger millet cv. CO (Ra). (**a**) 14 seeds were germinated on MS germination medium, (**b**) Germinated seed derived SAMs produced shoots, (**c**) multiple shoots were induced within 12 days of incubation in light within 4 days Source: Satish et al. (2017)

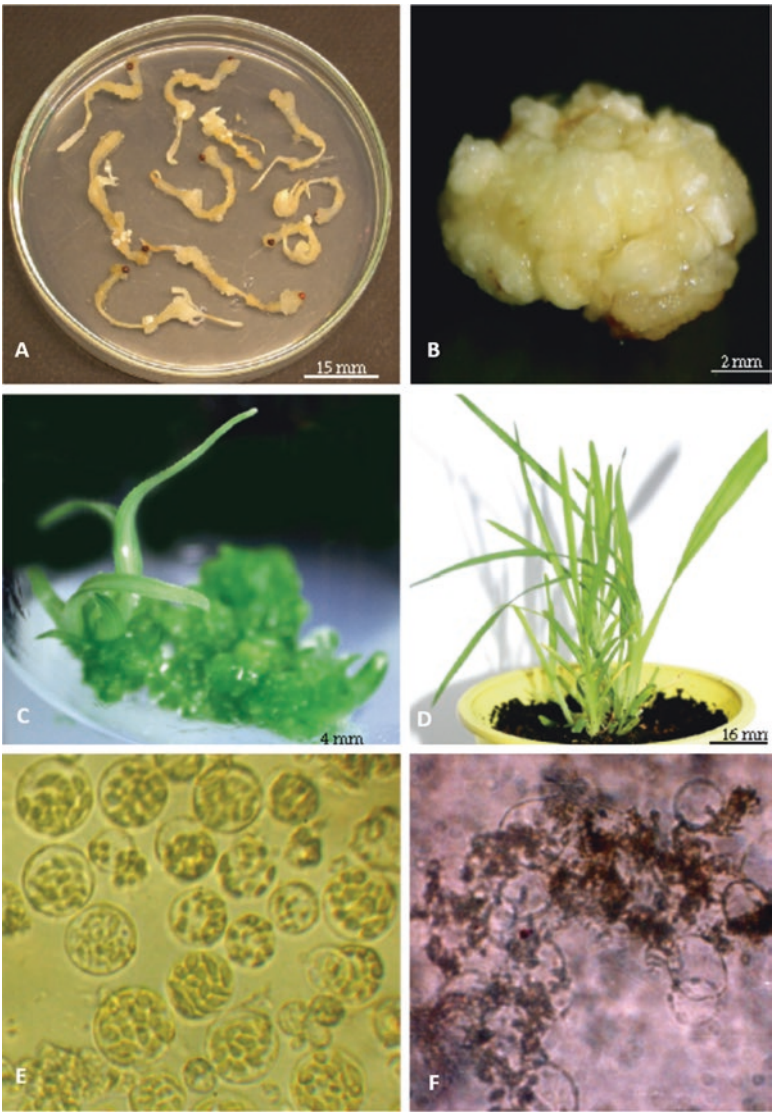

Fig. 3.8 (**a**) Callus induction from mesocotyl of *Eleusine coracana* from seed callus culture, (**b**) Morphology of compact, well-structured callus, (**c**) Plant regeneration of *E. coracana* from seed callus culture, (**d**) Rooted *E. coracana* plants in vitro, (**e**) *E. coracana* protoplasts isolated from seedlings, (**f**) Microcolonies formation in liquid KM8p medium
Source: Yemets et al. (2013)

although it is not commonly used in cereal callus induction. Yemets et al. (2013) also reported an efficient procedure for finger millet protoplast culture and induction of micronuclei with subsequent microprotoplast isolation of finger millet. Seedling coleoptiles were better sources of tissue for protoplasts isolation compared to callus cultures. An osmotic medium of mannitol and $CaCl_2$ (pH 5.5) and enzyme

solution of Cellulase (Onozuka R-10) and Pectolyase resulted in the best protoplast isolation. Microcolonies were visible 20–25 days after incubation on KM8p medium supplemented with amino acids, glutamine and proline.

The microprotoplast-mediated chromosome transfer (MMCT) technique is an asymmetric somatic hybridization method used for transferring alien chromosomes and genes (Ramulu et al. 1999). Polygenic traits or traits with unknown biochemical or molecular mechanisms (e.g. resistance to certain diseases or stresses and other economically important traits) are still recalcitrant to transfer using genetic engineering. This technique can be used for improvement of monocot plants by introducing agronomically-important genes, especially those that are recalcitrant to transfer i.e. polygenic traits or pathogenicity related traits, resulting in the production of chromosome addition lines (Saito and Nakano 2002; Yemets and Blume 2008). Yemets et al. (2013) established an effective method for induction (by antimitotic agents) and isolation of microprotoplast from finger millet somatic cells. The antimitotic drugs isopropyl N-(3-chlorophenyl) carbamate (CIPC) and cytochalasin B were used for microfilaments disruption and micronuclei induction in cells of finger millet seedlings.

3.10 Molecular Breeding

Crop improvement through conventional breeding is slow, especially for traits controlled by quantitative gene action like drought tolerance. Hence, the use of modern crop improvement tools such as genomics to transfer information about genes from model species to the species of interest, and genetic mapping in order to identify genes controlling traits of interest, can provide a more timely and robust response to crop production threats (Sorrells et al. 2003). It also provides added opportunities to develop crop cultivars with multiple stress tolerance.

Allele identification for agro-morphological traits and stress resistance is a major concern for improving productivity of finger millet. DNA-based microsatellite markers have been used to identify the agronomically-important traits such as days to flowering, plant height, peduncle length, ear exsertion, ear length, finger number, grain yield, disease resistance, drought resistance and nutritional quality. As finger millet is a hardy crop, it exhibits great morphological variation and is resistant to storage pests, it can prove important to identify QTLs related to climate resilience, storage-related and other important traits. Association-based QTL mapping gives a high resolution and several other advantages over the linkage mapping (Mott et al. 2000). Anchored, genomic and genic simple sequence repeat (SSR) markers have been used to map important QTLs e.g. 9 QTLs associated with Ca content were identified using 23 anchored SSR markers in 113 genotypes of finger millet (Kumar et al. 2015), 2 QTLs (OM5, FM8) for tryptophan content and 1 QTL (FMO2EST1) for protein content linked to opaque2 modifiers (*Opm*) gene in 190 genotypes using 120 genomic SSR markers (Babu et al. 2014b). Several agro-morphological trait-related QTLs have also been identified such as basal tiller number, days to 50%

flowering, flag leaf blade width, plant height, productive tillers, seed yield, leaf and neck blast resistance and number of tillers (Babu et al. 2014a, c; Ramakrishnan et al. 2016c). Ramakrishnan et al. (2017) identified 4 QTLs associated with root dry weight, shoot dry weight, and root length under P deficient and P sufficient conditions providing information to breed low P-tolerant genotypes in finger millet (Fig. 3.9). Recently, Babu et al. (2018) analyzed 66 accessions of the mini-core collection using 46 genomic and 58 genic SSRs markers. Significant associations were found for 20 agro-morphological traits (days to flowering, plant height, peduncle length, ear exsertion, ear length, length of longest finger, finger number, grain yield, finger blast). Two SSR markers designed from the blast resistance *Pi21* gene sequence of rice (FMBLEST35, FMBLEST36) were also found to be associated with blast disease resistance in finger millet.

3.11 Genomic Resources and Whole Genome Sequencing

The genomic resources available for *Eleusine coracana* are inadequate when compared with the major cereals crops. Less than 2000 expressed sequence tags (ESTs) are available, which is significantly lower than that of maize, rice and barley. A limited number of protein and nucleotide sequences are available (Table 3.4). Only 3 protein structures and 135 PopSets (sequence sets from phylogenetic and population studies) can be found. No complete gene, Unigene sequence or SNPs have yet been reported. A limited number of transcriptome studies have been carried out mainly for grain Ca content and a few stress conditions; however, most of these studies lack validation of sequence information and characterization of key genes. The recently released whole genome sequences (WGS) of finger millet will serve as a major basis to build these resources.

Recently, the whole genome sequence of about 1.2 Gb of two finger millet genotypes ML-365 (Hittalmani et al. 2017) and PR-202 (Hatakeyama et al. 2018) have been reported. Genotype ML-365, from the University of Agricultural Sciences, Bengaluru is a blast resistant and drought tolerant genotype with good cooking quality. Several drought responsive genes (2866), disease-resistance genes (R-genes) (1766) and genes related to calcium transport and accumulation (330) were identified. Genotype PR-202 (IC: 479099, NBPGR India accession number) was obtained from the University of Agricultural Sciences, Gandhi Krishi Vignan Kendra (GKVK), Bangalore and is resilience to drought and high-temperature stresses. The gene EcNAC1, the *Eleusine coracana* gene related to the drought response was also analyzed. The WGS availability can effectively be used for several strategies such as SNP identification, allele mining, identification and functional characterization of candidate genes related to agronomically-important traits and marker-assisted breeding programs.

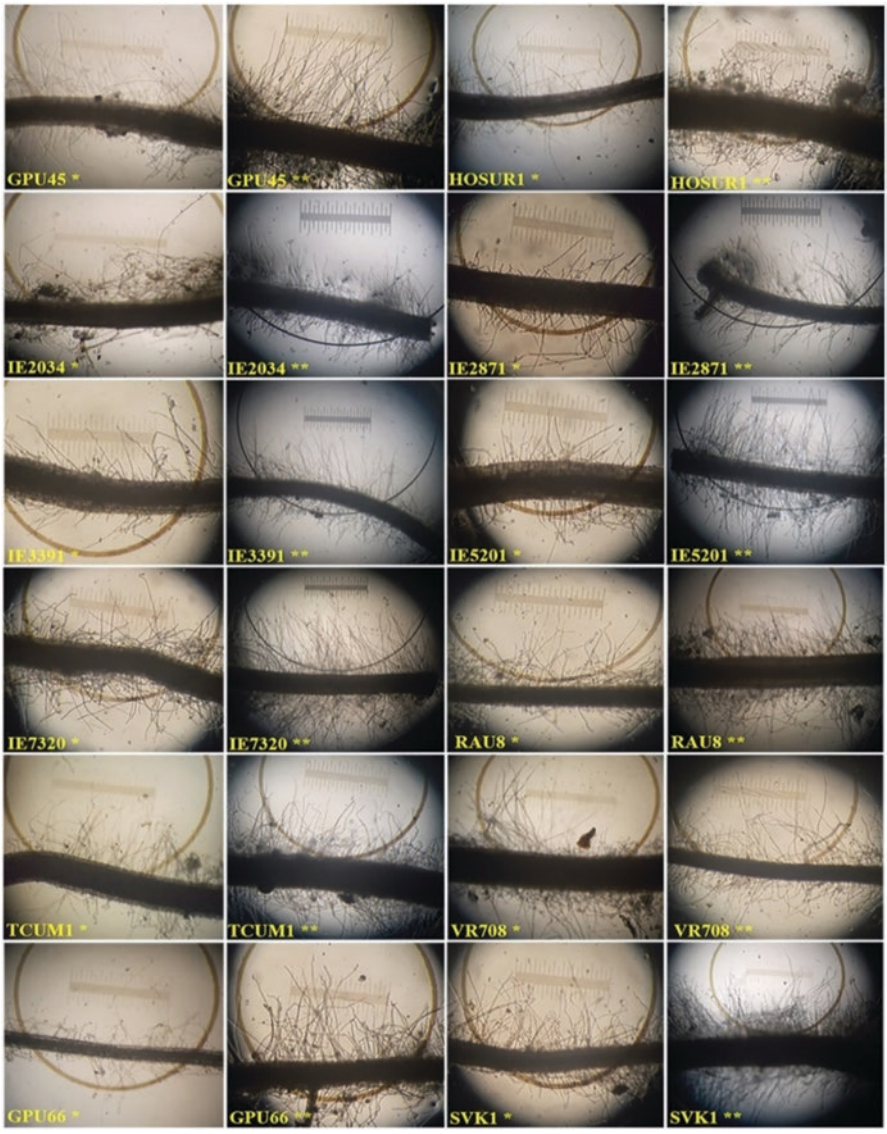

Fig. 3.9 Low phosphorous responding finger millet genotypes show low number of root hairs under P*suf* (∗ = P sufficient) and high number of root hairs P*def* (∗∗ = P deficient) conditions, respectively
Source: Ramakrishnan et al. (2017)

Table 3.4 Details on genomic and proteomic resources available for *Eleusine coracana*

Sequences/Resource	*Eleusine coracana* (No. of entries)
Expressed sequence tags (EST)	1934
Nucleotide	1111
Protein	559
PopSet	135
Protein structure	03
Identical protein groups	364
GEO datasets	06
BioProject	27
BioSample	243
Sequence Read Archive (SRA)	249
Probes	265
BioChem BioAssay	18

Source: NCBI (www.ncbi.nlm.nih.gov). Accessed September 2018

3.12 Genetic Improvement of Finger Millet Traits

3.12.1 Genetic Improvement for Herbicides Resistance

Bayer et al. (2014) developed *Eleusine coracana* lines resistant to dinitroaniline herbicides such as trifluralin, using mutant α-tubulin gene (*TUAm1*) isolated from dinitroaniline-resistant biotype of goosegrass *E. indica* (Blume et al. 2003; Yemets and Blume 2007). The mutant *E. indica* α-tubulin 1 (result of a single unique point mutation in both the alleles) confers an intermediate to high level of tolerance to a number of antimicrotubule herbicides, for example, dinitroanilines and phosphoroamidates. These herbicides have high affinity to plant tubulins. The team developed biobalistic (using tungsten particles with 0.7 μm diameter) and *Agrobacterium*-mediated systems for effective transformation of embryogenic calli of cvs. Tropikanka and Yaroslav 8. They demonstrated that the herbicide trifluralin resistance gene itself could be used as a selective marker gene in the selection of transgenic lines.

3.12.2 Genetic Improvement for Blast Resistance

The first successful transgenic finger millet plants were reported by Latha et al. (2005). They developed blast-resistant finger millet plants against the fungal pathogen *Pyricularia grisea* using a chemically synthesized gene based on prawn antimicrobial peptide (*PIN* gene). The shoot-tip derived embryogenic callus was transformed by the particle-inflow gun-mediated method. The stable integration of

multiple copies exhibited a high level resistance to leaf blast fungus. In a more recent report, leaf blast disease resistance transgenic finger millet plants have been developed by introducing the rice chitinase (*chi11*) gene (Ignacimuthu and Ceasar 2012). The rice chitinase gene has been frequently used for the production of fungal-resistant transgenic plants and not just in rice but in other crops as well such as peanut, mustard, cucumber, strawberry and American ginseng. The gene was introduced through *Agrobacterium*-mediated transformation using a plasmid pHyg-Chi.11 under the control of maize ubiquitin promoter. In both reports, the first progeny of transgenic lines produced resistant and susceptible plants in the ratio 3:1 confirming the normal Mendelian pattern of transgene segregation in both cases. No reports are available for neck and finger blast resistant or other disease-resistant transgenic finger millet. Screening of potential pathogenicity related genes and gene pyramiding will help in developing transgenic plants for a wider spectrum of diseases.

3.12.3 Genetic Improvement for Abiotic Stress Tolerance

Due to erratic weather and increasing climatic stress globally, it is important to develop increased stress tolerance in crops by overexpressing the gene of interest. Although finger millet is a hardy crop, it can be susceptible to drought, salinity and associated-oxidative stress especially at seed germination and early stages of seedling development. Jayasudha et al. (2014) developed salinity-tolerant finger millet GPU28 by expressing a double gene construct of *PgNHX1* (from *Pennisetum glaucum*) and *AVP1* (from *Arabidopsis thaliana*). At high salt concentrations, Na^+ causes ion toxicity (Tester and Davenport 2003) hence sequestration of excess cytosolic Na^+ into vacuoles is important to maintain ion homeostasis. The uptake of Na^+ ions is mediated by vacuolar Na^+/H^+ antiporter (NHX1) driven by the electrochemical gradient of protons generated by different vacuolar transporters such as H^+-PPase (AVP1) (Yamaguchi and Blumwald 2005). Several studies in different plant species indicate the importance of vacuolar antiporters, NHX1 and AVP1 in plant salt tolerance. The finger millet co-expressing PgNHX1 and AVP1 exhibited higher level of salinity tolerance (300 mM) compared to the wild type plants.

Osmotic adjustment and efficient scavenging of free radical generated during various abiotic stresses are important components of stress tolerance mechanisms in plants. Mannitol is an osmolyte known to scavenge hydroxyl free radicals and thereby minimize stress damage in several species. Hema et al. (2014) developed transgenic finger millet plants expressing the mannitol biosynthetic pathway gene from bacteria, mannitol-1-phosphate dehydrogenase (mtlD). The transgenic plants showed better growth, osmotic adjustment and chlorophyll retention under drought and salinity stress compared to wild types. The transgenic plants in both cases were developed using *Agrobacterium*-mediated transformation.

3.13 Conclusions and Prospects

Because of the increasingly dwindling agricultural land due to burgeoning population and industrialization, the world is expected to face a severe food demand by the end of 2050 (Gupta et al. 2017). Hence, there is an urgent need to increase the production of cereals. Finger millet should be given high priority in research and breeding programs as it can help meet all the challenging scenarios of malnutrition, water scarcity, extreme climatic conditions due to global warming and increasing disease susceptibility due to erratic weather. This C4 plant outperforms the C3 plants in harsh conditions and hence is an ideal crop for climate-resilient agriculture. It is a low-input crop and is often grown in infertile soils. This demands the need for identification of genotypes which have high fertilizer use efficiency, particularly N and P. There are only a few early-maturing cultivars which can mature in 90–95 days. Germplasm screening has provided some early flowering (50–52 days) cultivars and there is need to utilize these resources to develop early-maturing, photoperiod-insensitive cultivars suitable for different cropping systems. Breeding of dwarf varieties to avoid lodging and increase grain yield is also important. Finger millet is rich in micronutrients, especially calcium, iron and zinc, protein (especially the white grained varieties) and a good source of essential amino acids and antioxidants. The most cost-effective approach of mitigating *hidden hunger* is to introduce varieties with high Ca, Fe, Zn and protein content. The stress (drought, salinity, lodging) tolerant lines identified from multi-locational screening should be used to introgress the traits through breeding programs. Also, most of the cultivars of Africa origin are resistant to blast and storage pests. These cultivars are being used to transfer resistance to the susceptible cultivars through breeding. There is need of extensive and systematic work to identify the genes of interest and understanding the underlying genetic control and molecular physiological mechanisms of resistance and mineral accumulation. The availability of new genomic resources (WGS) of finger millet and knowledge of important trait governing genes can be combined with recent genome editing technology to develop nutritionally rich, climate resilient cultivars not only in finger millet but also in other important cereal crops.

Replacement of local cultivars by modern cultivars, a policy shift towards rice and wheat and other causes such as environmental degradation, urbanization, deforestation and bush fires have led to genetic erosion of indigenous species. Conventionally, efforts have been concentrated on conserving seeds in crop genebanks. However, it has become clear that the best strategy now is to combine ex situ approaches with the in situ conservation in their native agro-ecosystems and conservation of crop wild relatives. On-farm conservation ensures climate adaptability and evolution and is crucial for food and nutritional security. People world over are recognizing the health benefits of these once neglected coarse grains and hence are willing to pay high prices. Development of local niche markets for the indigenous landraces and their products can aid in their availability and popularity and can also ensure a premium price to conservationist farmers.

Appendices

Appendix I: Research Institutes Relevant to Finger Millet

Institute	Specialization and research activities	Website
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)	Research Program Dryland Cereals, Genebank repository	https://www.icrisat.org
All India Coordinated Research Project (AICRP), Indian Council of Agriculture Research (ICAR), India	Research program on Small Millets, Genebank repository	http://www.aicrpsm.res.in
National Bureau of Plant Genetic Resource (NBPGR), India	Research program on crop plants including small millets, Genebank repository	www.nbpgr.ernet.in
National Semi-Arid Resources Research Institute (NaSARRI), Uganda	Research in crops production for semiarid production systems in the areas of seed research and production management	www.nasarri.go.ug
Kenya Agricultural & Livestock Research Organization (KALRO), Kenya	Generating and promoting crops knowledge, information and technologies suitable for the region	www.kalro.org
Ethiopian Institute of Agricultural Research (EIAR), Addis Ababa, Ethiopia	Research to generate, develop and adapt agricultural technologies suited to Ethiopian Agricultural Research System	www.eiar.gov.et
Consultative Group for International Agricultural Research (CGIAR)	Research program on dryland cereals; crop improvement, crop management, postharvest technologies and market access to dryland cereal crops	http://gldc.cgiar.org/finger-millet/
Eastern and Central African Regional Sorghum and Millet Research Network (ECARSAM)	Enhance productivity, value adding and competitiveness of the ECA Subregional agricultural production system through increased production and productivity of sorghum and millet in quality and quantity	https://uia.org/s/or/en/
United States Agency for International Development (USAID)	Accelerated Value Chain Development (AVCD) Program -Drought Tolerant Crops (DTC) Value Chain	https://www.usaid.gov
International Livestock Research Institute (ILRI)	Bioversity social seeds – promoting open source seed systems for beans, forage legumes, millet and sorghum for climate change adaptation in Kenya, Tanzania and Uganda	https://www.ilri.org; http://data.ilri.org/portal/

Appendix II: Finger Millet Genetic Resources

Cultivar	Important traits	Cultivation location
GPU 26	Early, blast tolerant, suitable for late sowings and summer	India
GPU 45	Early, blast resistant	India
Chilika (OEB 10)	Moderately resistant to blast, resistant to stem borer	India
VL 315	Moderately resistant to finger and neck blast	India
GPU 48	Early, high yield, blast resistant	India
PRM-1	Resistant to blast	India
Bharathi (VR 762)	Moderately resistant to blast	India
GPU-67	Nonlodging (semi dwarf)	India
Srichaitanya (VR-847)	Moderately resistant to blast	India
KMR-301	High grain and straw yield, tolerant to blast	India
KOPN-235	Resistant to blast	India
OEB-526	Moderately resistant to leaf, neck and finger blast	India
OEB-523	Moderately resistant to blast; nonlodging; nonshattering	India
KMR-204	Early duration variety	India
VR936	Responsive to nitrogenous fertilizers	India
PPR2700 (Vakula)	Resistant to leaf blast and tolerant to drought	India
Indira Ragi-1	Non-shattering, nonlodging, responsive to fertilizers	India
VL-352	Moderately resistant to blast	India
Chattisgarh Ragi-2	Blast resistance; suitable for rainfed conditions	India
VL-376	Responsive to fertilizer; moderately resistant to blast	India
GNN-6	Moderately resistant to leaf and finger blast	India
GN-5	White grained; moderately resistant to leaf and finger blast	India
VL Mandua-348	Suitable for organic cultivation; resistant to neck and finger blast; tolerant to lodging	India
KMR-340	White grained; resistant to blast and blight diseases, tolerant to stem borer and aphids	India
Dapoli-2 (SCN-6)	High yielding, rich in iron and calcium; moderately resistant to blast; tolerant to aphids and *Spodopter littura*	India
CO-15	Highly responsive to nitrogenous fertilizer; non lodging; resistant to leaf, neck and finger blast	India
GNN-7	High mineral content (Ca, P, Mg)	India
VL-379	Resistant to neck and finger blast; moderately resistant to banded sheath blight; responsive to fertilizers	India
Chattisgarh Ragi-2 (BR-36)	Moderately resistant to neck and finger blast; tolerant to stem borer and other major pests	India
DHFM-78-3	Resistant to finger and neck blast; suitable for contingency planting	India
Engeny	High yielding	Africa
U15	High yielding; drought tolerant; blast resistant; *Striga* weed tolerant	Africa
P224	High yielding; blast resistant; tolerant to lodging	Africa

(continued)

Cultivar	Important traits	Cultivation location
Katumani	High yielding; dwarf variety; drought tolerant	Africa
Gulu E	High yielding	Africa
Okahale-1	High yielding; drought tolerant; blast resistant; *Striga* weed tolerant	Africa
Seremi 1	High yielding	Africa
Seremi 2	High yielding	Africa
Seremi 3	High yielding	Africa
Pese 1	High yielding	Africa
SX 8	High yielding	Africa
KNE 648	High yielding	Africa
SEC 915	High yielding	Africa
SEC 934	High yielding	Africa
IE 4115	High yielding	Africa
Tadesse	High yielding, drought resistant	Africa
Padet	High yielding	Africa
SDEV 87001	High yielding	Africa
Dalle-1 (IE-980)	Drought tolerant, nonlodging, susceptible to blast and *Cercospora* in rainy regions like Kaski	Nepal
Okhle-1 (NE1304-43)	Drought tolerant, nonlodging, field resistant to finger blast, neck blast and *Cercospora* leaf spot	Nepal
Kabre Kodo-1 (NF-6401-26)	Drought tolerant, nonlodging, field resistant to finger blast, neck blast and *Cercospora* leaf spot, tolerant to heavy rainfall	Nepal
Kabre Kodo-2 (GE-5176)	Drought tolerant, nonlodging, field resistant to finger blast, neck blast and *Cercospora* leaf spot	Nepal
Sailung Kodo-1 (GE-5016)	Nonlodging, moderately resistant to finger blast, neck blast and *Cercospora* leaf spot	Nepal
Yaroslav-8 (SE7)	Early; short height; high yielding; tolerant to low temperature	Ukraine

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