



History, Botanical and Taxonomic Description, Domestication, and Spread

1

Salej Sood , B. Kalyana Babu,
and Dinesh Joshi

Abstract

Finger millet (*Eleusine coracana* L. Gaertn) is an annual small-seeded cereal mainly grown in Africa and Asia for both grain and forage. Once considered an orphan crop for subsistence agriculture, it is today's mainstream crop due to its exceptional adaptation qualities and nutritional importance. The name "finger millet" is derived from the shape of its panicles, where spikes look like fingers and thumb. The crop is a domesticated cereal of African origin that spread in pre-history to Asia and is associated with cultural history. Archeological findings suggest Ethiopian highlands as a primary center of origin of the crop, and its domestication happened in western Uganda to the area extending Ethiopian highlands. A long history of cultivation and large variability of finger millet landraces makes India the secondary center of diversity for the crop. The genus *Eleusine* has about

nine species which are found across African, Asian, and South American tropical and subtropical areas. Studies on different species of *Eleusine* suggest that the cultivated gene pool diversity in finger millet in Africa has originated from the weedy progenitor *E. africana*.

Finger millet is an annual, small grain self-pollinated allotetraploid ($2n = 4x = 36$) plant mainly grown in two major continents, Africa and Asia (Sood et al. 2017, 2019). It has wide adaptability and its cultivation extends from sea level to higher elevations in the Himalayas (Gupta et al. 2012). Finger millet has the ability to grow under harsh conditions in diverse environments and has great food value in terms of nutritional profile. It is grown in dry and semi-dry regions for both grains and forage. The crop has exceptional adaptation under low moisture conditions and provides assured harvest under dry spells in marginal areas, suitable for contingency crop planning (Sood et al. 2016). The grains can be stored for years and have many health-promoting benefits besides a very good nutritional profile. The finger millet forage is also highly palatable and nutritious. At the global level among millets, finger millet occupies the fourth place, after major coarse grains, i.e., sorghum, pearl millet, and a minor millet, foxtail millet (Gupta et al. 2012).

Finger millet is a crop under the Poaceae family and Chloridoideae subfamily. It is the

S. Sood (✉)
ICAR-Central Potato Research Institute, Shimla
171001, HP, India
e-mail: salej.sood@icar.gov.in

B. K. Babu
ICAR-Indian Institute of Oil Palm Research,
Pedavegi, Andhra Pradesh, India

D. Joshi
ICAR-Vivekananda Institute of Hill Agriculture,
Almora, Uttarakhand, India

only millet that belongs to the tribe Chlorideae, whereas Piniceae is the tribe for all other millets. The finger millet panicles resemble the shape of the human thumb and fingers, therefore its English name has been given as “finger millet”.

Global estimates for precise area and production data on finger millet are not available. However, the literature estimates reveal that 5 million tons of finger millet grains were produced from 4 to 4.5 million ha area globally. The total production of finger millet in Africa was about 2 million tons, which was slightly lower than in India (2.2 million tons) (Sood et al. 2019). In Africa, finger millet is cultivated in eastern and southern African countries mainly Ethiopia, Kenya, Malawi, Tanzania, Uganda, Zaire, Zambia, and Zimbabwe. India and Nepal are the major finger millet producers in Asia, but the crop is also grown to some extent in China, Bhutan, Japan, and Sri Lanka. The latest estimates on area, production, and productivity of the crop in India are 67.2 thousand ha, 61.6 thousand tons, and 1332 kg/ha, respectively, which indicate a considerable decline in area, production, and productivity in comparison to previous years (Directorate of Economics & Statistics, Government of India, 2020, <https://eands.dacnet.nic.in/PDF/At%20a%20Glance%202019%20Eng.pdf>). Among various finger millet-producing states of India, Karnataka tops the list with >50% area, followed by Maharashtra and Uttarakhand (Chandra et al. 2020).

1.1 Origin and Phylogeny

Earlier botanists argued and suggested the origin of finger millet as India based on historical records and mention of finger millet by Sanskrit writers as ragi or rajika (De Candolle 1886; Dixit et al. 1987). Burkill (1935) proposed that *E. coracana* is the cultivated form ascended through selection in India from wild species *E. indica* (L) Gaertn. It was further stated that finger millet originated in India and Africa independently

(Vavilov 1951). More precise studies later explained that *E. coracana* is of African origin, domesticated in Western Uganda and Ethiopian highlands around 5000 years BC. The crop reached the Western Ghats in southern parts of India ~3000 BC (Hilu and De Wet 1976a; Hilu et al. 1979a, b; Fuller 2014).

The archaeological studies in Ethiopia dating back to the third millennium BC confirm the African origin of finger millet (Hilu et al. 1979a, b). Finger millet has two discrete races, African highland and Afro-asiatic lowland race. The former seems to be a derivative from *Eleusine africana*, which also resulted in the African lowland race. As per Hilu and De Wet (1976b), this African lowland race reached India as an Afro-Asiatic lowland race around 3000 BC. Wide phenotypic variability has been reported in African germplasm collections in comparison to Indian collections in many studies, strengthening the claim that Africa is the primary center of origin of finger millet. During its cultivation for years in the Indian subcontinent, the gene flow has resulted in great diversity in local and primitive crop cultivars, making India the secondary center of origin of the crop (Padulosi et al. 2009; Sood et al. 2016).

The cultivated finger millet species (*E. coracana*) is tetraploid with a basic chromosome number of 9 ($2n = 4x = 36$) (Sood et al. 2019). The species *E. africana* ($2n = 36$) exhibits great similarity with *E. coracana* in morphological features and gene flow occurs between them (Hilu and de Wet 1976b). First, the cytological studies showed that *E. indica* is one of the genome (AA) contributors to the cultivated species *E. coracana* and later chloroplast genome studies revealed *E. indica* to be the maternal genome donor of *E. africana*. The cytological studies also confirmed that *E. intermedia* and *E. tristachya* also belong to the genomic group “A” along with *E. indica* and these three species have a close genetic grouping (Mallikharjun et al., 2005). The results of genomic in situ hybridization and ribosomal DNA sites comparison on the

chromosomes of diploid and polyploid species inferred *E. indica* and *E. floccifolia* as two progenitors of *E. coracana* and *E. africana* (Bisht and Mukai 2000, 2001). Later, Neves et al. (2005) refuted *E. floccifolia* as a B genome donor based on genome analysis using nuclear internal transcribed spacers and plasmid trnT-trnF sequences. The results of molecular markers of *Pepc4* gene inferred that the species *E. coracana*, *E. africana* and *E. kigeziensis* are of allopolyploid origin (Liu et al. 2011), and strengthened the claim of two separate allopolyploidization origins for *E. africana*-*E. coracana* group and *E. kigeziensis*. However in both the cases, the diploid species group, *E. indica*-*E. tristachya* was recognized as the maternal parent (Liu et al. 2014), the paternal parents could not be traced for both the events as they might not exist now (Zhang et al. 2019). The placement of *Eleusine* in the subfamily Chloridoideae is undisputed.

1.2 Taxonomy and Classification

Eleusine is a small genus with 9–10 species distributed across continents mainly Africa, Asia, and South America in tropical and subtropical habitats (Hilu 1981; Phillips 1972). Out of the nine species, eight species, *E. coracana*, *E. africana*, *E. indica*, *E. kigeziensis*, *E. intermedia*, *E. multiflora*, *E. floccifolia*, and *E. jaegeri* (Phillips 1972) belong to East Africa, which is the center of diversity for the genus, *Eleusine*. The only species which has emerged outside Africa is *E. tristachya* (Neves 2011). This species is native to South America. The three species under the genus *Eleusine*, *E. coracana*, *E. tristachya*, and *E. indica* has wide adaptation ranging from sea level to high hills, while *E. jaegeri*, *E. floccifolia*, *E. kigeziensis*, *E. intermedia*, and *E. multiflora* are adapted to upland habitats and grow well in areas above 1,000 m amsl. Both diploid and polyploidy species are found in the genus *Eleusine* with three basic chromosome numbers ($x = 8, 9, 10$). The species has been classified into two separate groups, annual and perennial based on their growth habit.

The species under the genus *Eleusine* lack clear separation based on the taxonomic relationships, therefore, the gene pool does not have defined boundaries with respect to the primary, secondary, and tertiary gene pool species. However, phylogenetic studies in the *Eleusine* genus have categorized the species into three classes. Domesticated and wild forms of finger millet have been placed in the primary gene pool while diploid wild species progenitors constitute the secondary gene pool and all other species belong to the tertiary gene pool (Sood et al. 2019). The primary gene pool includes *E. coracana* subsp. *africana* and *Eleusine coracana* subsp. *coracana*, secondary gene pool comprises *E. indica*, *E. floccifolia*, and *E. tristachya* and the species *E. intermedia*, *E. jaegeri*, *E. kigeziensis*, *E. multiflora*, and *E. semisterlis* (syn. *E. compressa*) form the tertiary gene pool (Table 1.1).

The cultivated *Eleusine* form can be easily distinguished from wild forms based on its firm spikes and large and ball-shaped grains (Neves 2010). As discussed above, eight species of the *Eleusine* genus are native to Africa, which also includes the wild species *E. coracana* subspecies *africana* which has moved to America and Asia, particularly in warmer parts. Due to natural interbreeding between cultivated and wild finger millet species, many new hybrid combinations have appeared, most of which are lookalike companion weeds of the crop. This has been studied and demonstrated through scientific evidence using molecular markers that gene flow between subsp. *africana* and subsp. *coracana* has happened in nature (Dida et al. 2008).

1.3 *Eleusine* Germplasm Collections

India holds the largest germplasm collections of 10,507 accessions in the National Bureau of Plant Genetic Resources, New Delhi, under long-term conservation. Although most of these accessions belong to cultivated species and are indigenous, the collection also contains 6 wild species. ICRISAT in India holds about 5,957

Table 1.1 *Eleusine* species, habitat, and salient features

Species	Vernacular name	2n chromosome numbers & genome formula	Gene pool	Geographical distribution	Growth habit and important features
<i>Eleusine coracana</i> subsp. <i>coracana</i> (L.) Gaertn	Ragi, <i>Koracan</i> , <i>Coracan</i> , Kodra, Kodo, Mandal, Nachni, <i>Wimbi</i> , <i>Hawere</i> , <i>Khawke</i> , <i>Mulirubi</i> , <i>Mugumbi</i> , <i>Limbi</i> , <i>Lupodo</i> , <i>Malesi</i> , <i>Lipoke</i> , <i>Usanje</i> , <i>Mawe</i> , <i>Koddo</i> , <i>Bulo</i> , <i>Bule</i> , etc	36 (x = 9), AABB	Primary	Indian subcontinent (India, Nepal), East Africa (Uganda, Kenya, Ethiopia)	Growth habit—Annual; robust culm; digitate or subdigitate panicle/ inflorescence with 3–10 fingers, thick and firm, fingers straight or incurved and 4–14 cm long, width 9–15 mm Black, brown to reddish, and white globular grains used for food and fermented alcoholic drinks and therapeutic usages, straw is used as fodder
<i>E. coracana</i> subsp. <i>africana</i> Kennedy-O'Byrne	-	36 (x = 9), AABB	Primary	Africa, mainly in eastern and southern uplands (Malawi, Kenya, Rhodesia, Tanzania), and Arabia	Growth habit—Annual; moderately robust culm, up to 100 cm length; Glabrous soft leaves digitate or subdigitate panicle with 3–17 fingers, which are 3.5–15.5 cm long and 4–7 mm wide Black to brown ovate-oblong grains, which are about 1.2–1.6 mm long, It is a weed but used as a forage grass
<i>E. indica</i> (L.) Gaertn	Goosegrass, crows foot grass, wiregrass	18 (x = 9), AA	Secondary	Cosmopolitan weed of African origin; mostly tropics and subtropics	Growth habit—Annual; Slender culms; soft, glabrous leaves; digitate or subdigitate panicle with 3–8 narrow fingers, which are mostly straight and around 5–10 cm long, 3–6 mm wide; Elliptic black grains with conspicuous ridges on the surface It is a weed but used as a forage grass and has medicinal value
<i>E. floccifolia</i> (Forssk.) Spreng	<i>Akirma</i> , <i>akrma</i> , <i>dagoo</i> , <i>garrgorr</i>	18 (x = 9), BB	Secondary	Ethiopia, Somalia, Kenya, Yemen, Eritrea	Growth habit—Perennial; moderately robust tough culms with an approximate height of 20–70 cm; 8–55 cm long folded leaf blades; subdigitate

(continued)

Table 1.1 (continued)

Species	Vernacular name	2n chromosome numbers & genome formula	Gene pool	Geographical distribution	Growth habit and important features
					panicle with 2–10 fingers, which are mostly straight, 2.5–12 cm long, and 3.5–6 mm wide; Blackish elliptic to oblong grains, 0.9–1.4 mm long
<i>E. tristachya</i> (Lam.) Lam	–	18 (x = 9), AA	Secondary	South America, Brazil	Growth habit—short-lived Annual/Perennial; decumbent 10–45 cm long culms, internodes elliptical in section; 6–25 cm long and 1–4 mm wide leaf blades; digitate panicle with 2–3 straight fingers, fingers 1–4 cm long and 5–16 mm wide; dark brown to blackish oblong to trigonous grains with punctiform hilum; It is a weed but has potential as a fodder crop
<i>E. intermedia</i> (Chiov.) S. M. Phillips	–	18 (x = 9), AB	Tertiary	Kenya, Ethiopia	Growth habit—Perennial; moderately vigorous culms; herbaceous glabrous leaves; sub-digitate to a racemose panicle with 4–15 straight fingers, which are 5–12 cm long and 4–8 mm wide; black elliptic to trigonous grains
<i>E. jaegeri</i> Pilger	Manyata grass, <i>mafutiana</i> , <i>akirma</i> , <i>dagoo</i> , <i>titima</i>	20 (x = 10), DD	Tertiary	Tanzania, Uganda	Growth habit—Perennial; Vigorous culms; Leather-type leaves with rough margins; subdigitate or racemose panicle with 2–10 straight fingers, which are about 4–17 cm long and 3–7 mm wide; Black elliptic/ oblong to trigonous grains

(continued)

Table 1.1 (continued)

Species	Vernacular name	2n chromosome numbers & genome formula	Gene pool	Geographical distribution	Growth habit and important features
<i>E. kigeziensis</i> S. M. Phillips	–	36 (x = 9), AADD	Tertiary	Uganda, Congo, Burundi, Rwanda, Ethiopia	Growth habit—Perennial; Robust culms; Soft and Glabrous leaves; digitate panicle with 2–7 straight fingers, 7.5–14 cm long and 4.5–5.5 mm wide; Black elliptic to trigonous grains
<i>E. multiflora</i> Hochst. ex A. Rich	–	16 (x = 8), CC	Tertiary	Eritrea, Kenya, Ethiopia, Tanzania	Growth habit—Annual; Slender around 45 cm long culms; Soft, wide, and flat leaves; racemose panicle with 3–8 short wide curved fingers, 1–4 cm long and 8–16 mm wide; black oblong-compressed grains with a ridged surface; It is a weedy species but has potential as a valuable forage grass
<i>E. semisterilis</i> S. M. Phillips	–	Cytologically unknown	–	Kenya (Maybe extinct now)	Growth habit—Perennial; slender, erect, 145 cm high culms; leaf blades linear and loosely folded; subdigitate panicle with around 9 fingers which could be 5–15 cm long, laxly arranged spikelets in the fingers; black obovate grains

Source Phillips 1972; Liu et al. 2011; Sood et al. 2019; <http://www.theplantlist.org/browse/A/Poaceae/Eleusine/>

global accessions, of which 105 are of wild species. The major collection of wild species of finger millet is conserved and maintained at Agricultural Research Station, Griffin, Georgia, USDA, which has 17 wild species (*E. floccifolia*, *E. indica*, *E. jaegeri*, *E. multiflora*, and *E. tristachya*) out of the total collection of 766 accessions. Eastern Africa, which is the primary center of origin of the crop, Kenya, Zimbabwe, Uganda, and Zambia hold about 1902, 1158, 1155, and 497 accessions. Besides, many other South Asian

and African countries hold small germplasm collections (Sood et al. 2019). The global finger millet collection at ICRISAT has been characterized and core, as well as the mini-core set, have been developed for use in breeding and genomics studies (Upadhyaya et al. 2006). Although global diversity of finger millet has been conserved and important accessions have been identified, the wild species particularly, *E. coracana* subsp. *africana* and progenitors also need due attention (Neves 2010).

Based on compactness and shape of inflorescence, finger millet germplasm has been classified into races and subraces. The salient characters of races and subraces under each species are given in Table 1.2 (Prasada Rao et al. 1993; Bharathi 2011).

1.4 Crop Adaptation and Floral Biology

Finger millet has wide adaptation and can be grown in a wide habitat because of its hardy nature and short growing season. Being a C4 crop, it is highly efficient in adapting to environmental fluctuations and climate change. It can be grown from coastal plains to high hills, between 500 and 2,400 m above sea level (Fig. 1a). The genotype response although varies with agro-ecologies. Short-duration varieties are generally adapted to highlands and medium to long-duration cultivars do well in plains and tropical areas. The crop completes its life cycle in 75–160 days. It is generally grown in drylands as a rainfed crop but irrigated crop does well in terms of grain yield and the potential yield under irrigated conditions is around 5–6 t/ha. The crop can tolerate some waterlogging, but water stagnation severely affects crop productivity. Finger millet volunteers, shattering types are common in crop fields and difficult to identify early in the season. They look like normal plants but their seed starts shattering even in the immature stage itself.

The height of finger millet plants varies from 30 to 150 cm and mostly medium height cultivars are grown in India (100–130 cm). Finger millet inflorescence is in the whorl of 2–11 digitate, straight or slightly curved spikes (Fig. 1b and c). The spike is 8–15 cm long and 1.3 cm broad. In each spike, about 50–70 spikelets are arranged alternatively on one side of the rachis (Gupta et al. 2012). Each spikelet contains 3–13 florets. The florets have three stamens and the gynoecium is bi-carpellary, uni-locular with a superior ovary having two styles with feathery branched stigma (Seetharam et al. 2003). The anthers surround the stigma, which ensures self-

pollination. Finger millet grains vary in shape from round-oblong/oval, and white -reddish-brown in grain color (Fig. 1.2). The surface of finger millet grains is finely grooved and its pericarp is fused to the surface of the grain. Finger millet wild relatives have seed shattering trait, and at maturity seeds disperse naturally from the panicle, the cultivated species lost the seed shattering trait during domestication but it varies from cultivar to cultivar (de wet et al. 1984). Some cultivars are hard threshers while others still disperse some seed naturally at maturity.

The pollination system studies in finger millet revealed that pollen dust covers the stigma before it comes out of the lemma, leaving no or little chance for cross-pollination (Gupta et al. 2012). The spikelets opening follows the top to the bottom pattern in each spike, and florets in the spikelets open from bottom to top. The studies suggest that one floret in the spikelet opens per day. The flowering completes in around 5–7 days. Anthesis happens early morning between 1.00 and 5.00 a.m., when anthers dehisce to pollinate their stigmas (Gowda 1997). Dodake and Dhonukshe (1998) reported that pollen grains remain viable in finger millet for about 20 min, while stigma receptivity stays for up to 5 h. The estimation of natural crossing does not exceed 1% in finger millet (Seetharam 1998). Inter-varietal hybridization using the contact method (Ayyangar 1934) is the simplest and easiest way for recombination breeding. For successful hybridization, genotypes having dominant character such as pigmentation on nodes are used as the male parent. This helps in the identification of true hybrids in the F₁ generation. However, inducing male sterility through hot water treatment for 5 min at a temperature of 48–52 °C of immature inflorescence on the 3rd to 4th day of emergence was effective in getting few true hybrid seeds (Sood et al. 2019). Genetic male sterility (GMS) and partial GMS source have been identified in the crop but are of little use due to maintenance problem and varying level of sterility/fertility in different locations (Gupta et al. 1997; Gowda et al. 2014; Sood et al. 2019).

Table 1.2 Races and subraces in finger millet germplasm and their features

Species	Subspecies	Race	Subrace(s)	Salient features
<i>E. Coracana</i>	<i>Coracana</i>	<i>Elongata</i>	<i>liliaceae, stellata, incurvata, and digitata</i>	This race is commonly found in Africa and Asia. It has long slender 10–24 cm long panicles with digitately arranged spreading fingers, which curve outward on maturity. In the subrace <i>liliaceae</i> , the fingers in the panicle are reflexed, while subrace <i>stellata</i> contains twisted fingers. As the name suggests, subrace <i>incurvata</i> have incurved fingers that give a fist-like appearance, and subrace <i>digitata</i> has top curved fingers
		<i>Plana</i>	<i>seriata, confundere, and grandigluma</i>	This race <i>plana</i> has large 8–15 mm long spikelets, which are arranged on the rachis as even rows of two and look like a flat ribbon. The subrace <i>seriata</i> has serially arranged spikelets on the rachis, which gives ribbon-like appearance, the subrace <i>confundere</i> contains numerous fertile florets which upon grain filling at maturity give a compact look to the panicle, the <i>grandigluma</i> subrace is characterized by very large pointed glumes, which are longer than spikelets
		<i>Compacta</i>		The race <i>compacta</i> members are commonly stated as cockscomb finger millets. The spikelets have 9 or more florets. Fingers incurve at the tip to form a fist-like panicle
		<i>Vulgaris</i>	<i>laxa, reclusa, and sparsa</i>	The race <i>vulgaris</i> is the most distinct among all the four races of finger millet based on phenotype. It has long slender panicle branches, which are arranged digitately, and spikelets have 4–8 florets. The moderate number of florets in the spikelets give a semi-compact appearance and fingers incurve at maturity. As the name suggests, <i>laxa</i> subrace has long open fingers and spikelets arranged in thin rows on the rachis of the panicle fingers. This subrace resembles the wild <i>Africana</i> race. The subrace <i>reclusa</i> is characterized by short open fingers, which do not curve. The <i>sparsa</i> subrace is also characterized by open fingers, however, the spikelets arrangement on the panicle has naked space in between the clusters of spikelets
<i>E. africana</i>	<i>africana</i>	<i>africana</i>	–	The panicles in the race <i>africana</i> are long and thin, i.e., around 8–17 cm long and about 5 mm wide. The spikelets on the rachis are arranged in two rows on one side with 4–9 flowers. The glumes are short <5 mm, smaller than the spikelet
		<i>spontanea</i>	–	The features of race <i>spontanea</i> match with race <i>africana</i> . The race <i>spontanea</i> contains derivatives of hybridization between <i>E. coracana</i> and <i>E. africana</i>

Source Bharathi (2011)



Fig. 1.1 Finger millet crop in Uttarakhand hills, India. **a** Crop stand of improved variety VL 376. **b** Immature panicles of finger millet variety VL 376. **c** Mature panicles of finger millet variety VL 376

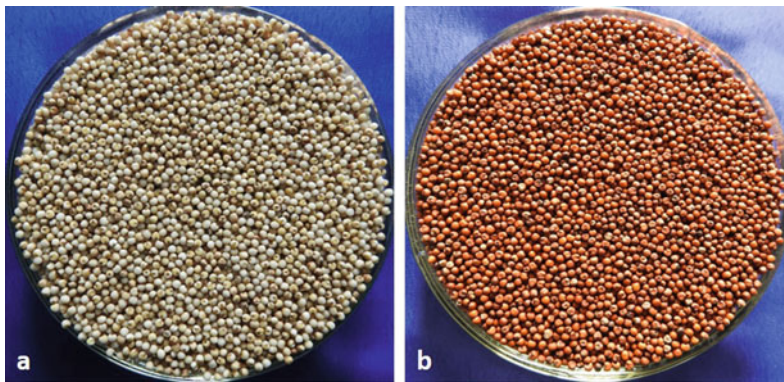


Fig. 1.2 Cleaned finger millet grains after threshing. **a** White grains of finger millet variety VL 382. **b** Reddish-brown grains of finger millet variety VL 376

1.5 Genome Size

Using Feulgen microspectrophotometry, nuclear DNA content of *Eleusine* spp. was first reported by Hiremath and Salimath (1991), which was later substantiated by Mysore and Baird (1997) with more accurate analysis using laser flow cytometry. The 2C DNA content of different *Eleusine* species varied from 1.51 to 3.87 pg. The cultivated species, *E. coracana* was found to have 3.36–3.87 pg 2C DNA followed by *E. coracana* subsp. *africana* (3.34 pg), *E. indica* (1.61–1.76 pg), *E. tristachya* (1.51 pg), *E. floccifolia* (2.0 pg), *E. multiflora* (2.65 pg), and *E. jaegeri* (1.90 pg). A recent study reported 1.20, 1.84, 1.14, 1.21, 2.52 pg 2C DNA content in *E.*

jaegeri, *E. multiflora*, *E. tristachya*, *E. indica*, and *E. coracana* subsp. *africana*, respectively (Hittalmani et al. 2017). In their study, the cultivated species *E. coracana* was found to have 3.01 pg 2C DNA content and 1453 Mb genome size. The analysis of genome size of wild species showed a range of 580 Mb in *E. jaegeri* to 1217 Mb in *E. coracana* subsp. *africana*. *E. coracana* subsp. *Coracana*, and *E. coracana* subsp. *africana* were found to have almost similar genome size which was attributed to the domestication of *E. coracana* subsp. *coracana* from *E. coracana* subsp. *africana* (Hittalmani et al. 2017). Although in comparison to many types of grass and other plants, the genome size of the *Eleusine* species is small, still it is too large for genomics studies (Neves 2010).

1.6 Genetic Improvement

This spatial isolation of the crop in India and Africa has led to the appearance of two genetically and morphologically diverse gene pools. However, studies conducted on genetic diversity in African and Indian collections presented much larger variation for inflorescence color in African accessions in comparison to Indian collections. Many studies conducted on the phenotypic evaluation of Indian and African germplasm showed wide variation for inflorescence types in both gene pools. The studies reported that most Indian accessions inflorescence belong to race *vulgaris*, i.e., they have semi-compact to compact ears while varied ear types extending from open to fist-shaped, mostly belonging to two major races *plana* and *compacta* were found in African accessions. Accessions in both the gene pools also vary for many quantitative traits (Naik et al. 1993). More diversity in the African gene pool has been attributed to gene flow from wild species *E. africana* into cultivated finger millet.

Various DNA-based molecular markers have been used to study the genetic diversity of the finger millet gene pool. Both genomic and genic simple sequence repeat (SSR) markers have been used markers for profiling finger millet accessions to study the genetic diversity. Due to the nonavailability of SSRs earlier studies used random amplified polymorphic DNA (RAPD) markers. Most of these studies clustered the finger millet accessions into two major groups, belonging to two distinct gene pools, i.e., African and Indian gene pools. In a study of Indian accessions, DNA markers could clearly classify accessions of North India and southern India. The South Indian accessions were found to be genetically close to African accessions. The results of genetic diversity studies substantiate that accessions of southern India are closer to African genotypes due to their origin from wild species *E. africana*, however, the north and northeast accessions are different and the uniqueness of such gene pool needs to be explored (Panwar et al. 2010a, b).

The introduction and use of African germplasm in India resulted in a higher genetic gain in finger millet breeding. Indo-African crosses in finger millet generated more variability and diverse parents resulted in higher productivity of finger millet, which increased >50% in Karnataka State and around 60 percent in Tamil Nadu State in India (Seetharam 1982; Nagarajan and Raveendran 1983). Blast is the major biotic stress affecting finger millet productivity and the identification of stable sources of resistance is the key to developing resistant genotypes. Screening of diverse germplasm particularly African germplasm has resulted in the identification of stable sources of resistance for the blast in finger millet, which has been used to develop resistant varieties through recombination breeding (Seetharam 1998). To date, more than 30 finger millet varieties have been released in India, where the major breeding objectives were maturity duration, grain yield, fodder yield, and disease resistance. The least emphasis was laid on nutritional quality traits earlier but now the nutritional quality is the integral component of finger millet breeding programs in India and Africa.

References

- Ayyangar GNR (1934) Recent work in the genetics of millets in India. *Madras Agric J* 22:16–26
- Bharathi A (2011) Phenotypic and genotypic diversity of global finger millet (*Eleusine coracana* (L.) Gaertn.) composite collection. PhD thesis, Tamil Nadu Agricultural University, Coimbatore, India
- Bisht MS, Mukai Y (2000) Mapping of rDNA on the chromosomes of *Eleusine* species by fluorescence in situ hybridization. *Genes Genet Syst* 75:343–348
- Bisht MS, Mukai Y (2001) Genomic in situ hybridization identifies genome donor of finger millet (*Eleusine coracana*). *Theor Appl Genet* 102:825–832
- Burkill IH (1935) A dictionary of economic products of Malaya peninsula. Crown Agents of the Colonies, London
- Chandra AK, Chandora R, Sood S, Malhotra N (2020) Global production, demand and supply. In: Singh M, Sood S (eds) *Millets and pseudo-cereals-genetic resources and breeding advancements*. Woodhead Publishing, Elsevier, pp 7–18

- De Candolle A (1886) Origin of cultivated plants. Hafner Publishing Co., New York
- deWet JMJ, Prasada Rao KE, Brink DG, Mengesha MH (1984) Systematic evolution of *Eleusinecoracana* (Gramineae). *Amer J Bot* 7:550–557
- Dida MM, Wanyera N, Dunn MLH, Bennetzen JL, Devos KM (2008) Population structure and diversity in finger millet (*Eleusine coracana*) germplasm. *Trop Plant Biol* 1:131–141
- Dixit A, Dixit SS, VishnuMittre (1987) The occurrence of *Eleusine africana* Kennedy-O' Byrne in India and its significance in the origin of *Eleusine coracana*. *Proc Indian Acad Sci (plant Science)* 85:1–10
- Dodake SS, Dhonukshe BL (1998) Variability in floral structure and floral biology of finger millet (*Eleusine coracana* (L.) Gaertn.). *Indian J Genet* 58:107–112
- Fuller DQ (2014) Finger millet: origins and development. In: Smith C (ed) *Encyclopedia of global archaeology*. Springer, pp 2783–2785. <https://doi.org/10.1007/978-1-4419-0465-2>
- Gowda BTS (1997) Genetic enhancement and breeding strategies in finger millet (*Eleusine coracana* Gaertn.). In: National seminar on small millets, 23-24 April 1997, Coimbatore, India, pp 16–18 (Extended summaries)
- Gowda MVC, Pushpalatha N, Jhadav SS, Satish RG, Boronayaka MB, Sujay V, Pramila CK, Manasa KG, Gowda J, Ravishankar P, Krishnappa M, Narasimhamurthy DN (2014) PS-1 (IC0598201; INGR14015), a finger millet (*Eleusine coracana*) germplasm with partial sterility, useful in hybridization and easy maintenance. *Indian J Plant Genet Resour* 27(2):192
- Gupta SC, Muza FR, Andrews DJ (1997) Registration of INFM 95001 finger millet genetic male sterile line. *Crop Sci* 37:1409
- Gupta A, Sood S, Agrawal PK, Bhatt JC (2012). Floral biology and pollination system in small millets. *Eur J Plant Sci Biotechnol* 6(2):80–86
- Hilu KW (1981) Taxonomic status of the disputable *Eleusine compressa* (Gramineae). *Kew Bull* 36:559–562
- Hilu KW, De Wet JMJ (1976a) Domestication of *Eleusinecoracana*. *Econ Bot* 30:199–208
- Hilu KW, DeWet JMJ (1976b) Racial evolution of finger millet, *Eleusine coracana*. *Amer J Bot* 63:1311–1318
- Hilu KW, De Wet JMJ, Harlan JR (1979a) Archaeobotanical studies of *Eleusine coracana* ssp. *coracana* (finger millet). *Amer J Bot* 63:330–333
- Hilu KW, deWet JMJ, Harlan JR (1979b) Archaeobotany and the origin of finger millet. *Amer J Bot* 66:330–333
- Hittalmani S, Mahesh, HB, Deepak Shirke M, Biradar H, Uday G, Aruna YR, Lohithaswa HC, Mohanrao A (2017) Genome and Transcriptome sequence of Finger millet (*Eleusine coracana* (L.) Gaertn.) provides insights into drought tolerance and nutraceutical properties. *BMC Genomics* 18:465. <https://doi.org/10.1186/s12864-017-3850-z>
- Hiremath SC, Salimath SS (1991) Quantitative nuclear DNA changes in Eleusine (Gramineae). *Pl Syst Evol* 178:225–233
- Liu Q, Jiang B, Wen J, Peterson PM (2014) Low-copy nuclear gene and McGISH resolves polyploid history of *Eleusine coracana* and morphological character evolution in Eleusine. *Turkish J Bot* 38:1–12
- Liu Q, Triplett JK, Wen J, Peterson PM (2011). Allotetraploid origin and divergence in Eleusine (Chloridoideae, Poaceae): evidence from low-copy nuclear gene phylogenies and a plastid gene chronogram. *Ann Bot-London* 108:1287–1298
- Mysore KS and Baird V (1997) Nuclear DNA content in species of Eleusine (Gramineae): a critical re-evaluation using laser flow cytometry. *Plant Syst Evol* 207:1–11
- Nagarajan C, Raveendran TS (1983) Germplasm mobilization and utilization in finger millet in Tamil Nadu. National Seminar on Finger Millet-Genetics and Breeding, UAS, Bangalore, India
- Naik BJ, Shankare Gowda BT, Seetharam A (1993) Pattern of variability in relation to domestication of finger millet in Africa and India. In: Riley KW, Gupta SC, Seetharam A, Mushonga JN (ed) *Advances in small millets*, Oxford and IBH Publishing Co. Pvt. Ltd. New Delhi, pp 347–364
- Neves SS (2011) Eleusine. C. Kole (ed.), *Wild Crop Relatives: Genomic and Breeding Resources, Millets and Grasses*, Springer-Verlag Berlin Heidelberg, pp 113–133
- Padulosi S, Bhag Mal, BalaRavi S, Gowda J, Gowda KTK, Shanthakumar G, Yenagi N and Dutta M (2009) Food Security and Climate Change: Role of Plant Genetic Resources of Minor Millets. *Indian J Plant Genet Res* 22(1):1–16
- Phillips SM (1972) A survey of the Eleusine Gaertn. (Gramineae) in Africa. *Kew Bull* 27:251–270
- Panwar P, Saini RK, Sharma N, Yadav D, Kumar A (2010a) Efficiency of RAPD, SSR and cytochrome P450 gene based markers in accessing genetic variability amongst finger millet (*Eleusine coracana*) accessions. *Mol Biol Rep.* 37(8):4075–4082. <https://doi.org/10.1007/s11033-010-0067-5>
- Panwar P, Nath M, Yadav VK and Kumar A (2010b) Comparative evaluation of genetic diversity using RAPD, SSR and cytochrome P450 gene based markers with respect to calcium content in finger millet (*Eleusine coracana* L. Gaertn.). *J Genet* 89:121–133. <https://doi.org/10.1007/s12041-010-0052-8>
- Prasada Rao KE, De Wet JMJ, Gopal Reddy V, Mengesha MH (1993) Diversity in the small millets collection at ICRISAT. In: Riley KW, Gupta SC, Seetharam A Mushonga JN (ed) *Advances in Small Millets*, Oxford & IBH Publishing Co, New Delhi, India pp 331–346
- Seetharam A (1982) Finger millet improvement. *Indian Farming* 32(3):3–6
- Seetharam A (1998) Small millets research: achievements during 1947-97. *Indian J Agricul Sci* 68 (8):431–438

- Sood S, Joshi DC, Chandra A, Kumar A (2019) Phenomics and genomics of finger millet: current status and future prospects. *Planta*. <https://doi.org/10.1007/s00425-019-03159-6>
- Sood S, Kant L, Pattanayak A (2017) Finger millet (*Eleusine coracana* (L.) Gaertn.)-A minor crop for sustainable food and nutritional security. *Asian J Chem* 29(4):707–710
- Sood S, Kumar A, Babu BK, Gaur VS, Pandey D, Kant L, Pattanayak A (2016) Gene discovery and advances in finger millet [*Eleusine coracana* (L.) Gaertn.] genomics-an important nutri-cereal of future. *Front Plant Sci* 7:1634. <https://doi.org/10.3389/fpls.2016.01634>.
- Upadhyaya HD, Gowda CLL, Pundir RPS, Reddy VG, Singh S (2006) Development of core subset of finger millet germplasm using geographical origin and data on 14 quantitative traits. *Genet Resour Crop Evol* 53:679–685
- Vavilov NI (1951) The origin, variation, immunity and breeding of cultivated plants. The Roland Press Co., New York
- Zhang H, Hall N, Goertzen LR, Chen CY, Peatman E, Patel J and McElroy JS (2019) Transcriptome analysis reveals unique relationships among *Eleusine* species and heritage of *Eleusine coracana*. *G3: Genes Genomes Genetics* 9:2029–2036. <https://doi.org/10.1534/g3.119.400214>