Floral Biology, Pollination, Genetics, Origin, and Diversity in Barnyard Millet

23

Rumana Khan, Akhouri Nishant Bhanu, N. Aneesha, H. Sirisha, A. R. S. S. H. Gupta, and A. D. S. S. Ajay Nikhil

Abstract

Barnyard millet (*Echinochloa* spp.) has emerged as one of the earliest indigenous millets throughout the semi-arid tropical regions of Asia and Africa. Communities belonging to hilly and tribal regions in Asia, particularly in India, China, and Japan, cultivate two main species for food and fodder: *Echinochloa esculenta* (A. Braun) H. Scholz; syn. *E. utilis* Ohwi Yabuno (Japanese barnyard millet) and *Echinochloa frumentacea* Link; syn. *E. colona* var. *frumentacea* (Link) Ridl. Due to its short life cycle, the crop has an extensive range of adaptations and occupies a specialized niche in marginally humid regions. Despite the crop's endurance to withstand harsh conditions, its importance had been denied substantially over the last 50 years. It serves as a superior alternative during famine periods. In the Indian Himalayan region, the crop appeared to be utilized as a substitute for rice. It has been established to be a great choice for climate-resilient agriculture. It is a functional food crop because of its high nutrient content and antioxidant properties. Because the crop's grains are so incredibly nutritious, demand for it has recently surged. Therefore, it has the potential to ensure both nutritional as well as food security, particularly in high-terrain regions where deficiencies in nutrients are frequent. Despite its enormous potential, the crop has not achieved widespread acceptance and remains visible only as sustenance for the underprivileged. In order to make the crop competitive and modernize its production, this effort aims to consolidate the scant knowledge on agricultural history, domestication, phylogeny, plant architecture, and floral biology of the crop that will be of use to the readers and researchers working on this crop.

R. Khan (✉) · A. N. Bhanu · N. Aneesha · H. Sirisha · A. R. S. S. H. Gupta · A. D. S. S. Ajay Nikhil
Department of Genetics and Plant Breeding, College of Agriculture, Rani Lakshmi Bai Central Agricultural University, Jhansi, Uttar Pradesh, India

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23.1 Barnyard Millet

Barnyard millet, *Echinochloa* sp. ($2n = 36, 54$), grown as a cereal fodder crop, is one of the oldest domesticated millets in the semi-arid tropics of Asia and Africa. Barnyard millet is a self-pollinated crop which belongs to the family Poaceae, subfamily Panicoideae, and tribe Paniceae (Kellogg 2015). It is constituted as the fastest-growing millet crop and is typically grown on hill slopes and undulating fields in mountainous, tribal, or backward areas where crop choice and possibilities are constrained. The genus *Echinocholoa* includes 35 wild species spread over the world. Among these, *E. utilis* (A. Braun) H. Scholz; syn. *E. utilis* Ohwi et Yabuno also known as the Japanese barnyard millet and *E. frumentacae* Link; syn. *E. colona* var. *frumentacea* (Link) Ridl., also known as Indian barnyard millet or sawa millet, are the two domesticated species. *E. utilis* is a temperate annual hexaploidy ($2n = 6x = 54$). *E. frumentacae* ($2n = 36, 54$) are cultivated as minor cereals in Japan, Korea, the north-eastern parts of China and India, Pakistan, and Nepal, respectively (Yabuno 1987).

Barnyard millet is cultivated in India for human consumption as well as livestock feed. Barnyard millet production is often preferred in areas where climate and environmental factors are inappropriate for raising and cultivating of rice crop (Yabuno 1987). It is largely grown in India in two separate agroecologies, one in Tamil Nadu's Deccan plateau area and the other in Uttarakhand's mid-hills of the Himalayas in the north. The second-most significant small millet in India after finger millet, barnyard millet has production and productivity of 0.147 mt and 1034 kg/ha, respectively. It has received considerable interest as a fodder crop in the United States and Japan due to its early growth and maturity. Barnyard millet has drawn attention recently, largely due to its excellent nutritional content.

23.1.1 History, Origin, and Domestication

Echinochloa frumentacea, which likely evolved in both India and Africa, followed a comparable evolutionary path on both continents. It is cultivated annually in Malawi, Tanzania, the Central African Republic, and India (Doggett 1989). *E. colona* (L.) Link, also known as tropical grass, is the wild progenitor of *E. frumentacea*, sometimes referred to as jungle rice. It is raised for beer, fodder, and grain. It varies from *E. esculenta* due to the presence of white caryopses and correspondingly tiny embryos, while *E. esculenata* has brownish caryopses and longer pedicels.

Annual *Echinochloa esculenta* is mostly grown in temperate areas of Japan, Korea, China, Russia, and Germany (de Wet et al. 1983). Around 4000 years ago in Japan, it was directly domesticated from barnyard grass (*Echinochloa crusgalli* (L.) Beauv) (Doggett 1989).

From a number of investigations, Yabuno (1962, 1984, 1966, 2001) provided a good grasp of this genus. Two domesticated species, *E. esculenta* (Japanese barnyard millet) and *E. frumentacea* (Indian barnyard millet), are closely related to their wild counterparts, *E. crus-galli* and *E. colona*. Both domesticated species and their predecessors are hexaploid ($2n = 6x = 54$, where $x = 9$) (Yabuno 1962, 1966).

Interspecific hybrids of *E. crusgalli* with *E. esculenta* and *E. colona* with *E. frumentacea* have been determined to have a typical meiotic division with 27 bivalents. Crosses between these two groups are sterile and generate micronuclei, univalents, and laggards throughout the meiotic process. These cytogenetic findings indicate that the cultivated species *E. utilis* and *E. frumentacea* are derived from two different hexaploid wild species, *E. colona* and *E. crusgalli* (Yabuno 1966).

Based on a comparison of their complete chloroplast (cp) genomes, both *E. crusgalli* and *E. colona* comprise 136 genes in their chloroplast genomes. However, phylogenetic studies revealed that *E. colona* diverged from *E. oryzicola* and *E. crusgalli* between 2.65 and 3.18 million years ago, respectively (Guo et al. 2017). Based on indication of awn or awnless trait, minute differences in the spikelets, and glume morphology differentiated Japanese and Indian barnyard millet (de Wet et al. 1983). In contrast to *E. esculenta's* big, typically awned spikelets with chartaceous upper glumes and lower lemma, *E. frumentacea* bears smaller, awnless spikelets with membranous glumes.

Echinochloa in temperate East Asia has been grouped into three classified polyploid categories:

Group	Species	Ploidy
E. oryzicola complex	Two forms of *E. oryzicola*, *E. persistentia* (non-shattering form of *oryzicola*), and cultivated forms of *E. oryzicola* and *E. phyllopogon*	Allotetraploid
E. crus-galli complex	*E. crus-galli* var. *crus-galli*, *E. crus-galli* var. *praticola*, *E. crus-galli* var. *formosensis*, *E. oryzoides*, *E. esculenta* (Japanese barnyard millet), and Lijiang millet (a cultivated form from China)	Allohexaploid
Echinochloa colonum complex	*E. colonum* and *E. frumentacea* (Indian barnyard millet)	Allohexaploid

23.1.2 Cytogenetics

The genus *Echinochloa* reflects an estimated 25 or more perennial or annual species, majority of those are weeds in paddy fields. In this species, the fundamental chromosomal number is $x = 9$. The diploid *E. obtusiflora* Stapf ($2n = 2x = 18$), the tetraploid *E. oryzicola* Vasing ($2n = 4x = 36$), and the hexaploid *E. untilis* Ohwi ($2n = 6x = 54$) are polyploid species in this genus. Yabuno (1962) documented inter-specific polyploidy in a number of cytotypes ($2n = 4x = 36$, $6x = 54$, $7x = 63$,

$12x = 108$, and $14x = 126$). The Japanese barnyard millet (*E. esculenta*) and Indian barnyard millet (*E. frumentacea*) are closely linked to the wild relatives of the barnyard millet species *E. crusgalli* and *E. colona*. Like their domesticated relatives, these species are hexaploids with the basic chromosomal number $x = 9$ ($2n = 6x = 54$).

With the formation of 27 bivalents, the interspecific crossings between the domesticated species (*E. crusgalli* × *E. esculenta* and *E. colona* × *E. frumentacea*) and their wild relatives displayed typical meiotic behavior. Crosses between cultivated ones and their progenitors, on the contrary, exhibited meiotic abnormalities (formation of univalents, laggards, and micronuclei). Based on cytological evidence, *E. crusgalli* and *E. colona* are presumably the progenitors of *E. esculenta* and *E. frumentacea*.

The wild species is allohexaploid and shares two of its three genomes with *E. crusgalli* due to the 18 bivalents and 9 univalents resulting from crossing *E. crusgalli* and *E. oryzoides*. This demonstrates that the tetraploid *E. oryzoides* and the *Echinochloa* species that have not yet been named spontaneously hybridized to produce *E. crusgalli* (Yabuno 1966, 1984; Sood et al. 2015). These results were also validated by using DNA sequences from the chloroplast and internal transcribed spacer (Ye et al. 2014).

23.2 Botanical Description

Barnyard millet is extensively distributed in the high-temperature regions around the world due to its profound adaptability. By the heat of summer, it can exceed an altitude of 2000 m above mean sea level (Gupta et al. 2009).

It is a hardy annual crop plant that can attain the heights of 220 cm. Compared to other small millets, it develops rapidly, has a relatively short growth period, and finishes the life cycle within 45–60 days (Sood et al. 2015). It could take a little longer to mature in the northern hill habitat. The leaf blades are flat, broad, and ligule-free. The inflorescence is a terminal panicle which is 10–25 cm long, is composed of dense racemes with 3–4-mm-long spikelets (Sood et al. 2015) and it can be compact, intermediate, or open in size, color (green, light purple, and dark purple), and shape (cylindrical, pyramidal, globose to elliptic) (Renganathan et al. 2017; Kuraloviya et al. 2019). The inflorescence seldom droops and is typically upright. Racemes differ in size from a few to many (22–64 per inflorescence), are full of numerous spikelets arranged in four arbitrary rows on the triquetrous rachis, and are freely or strongly attached to the rachis (Renganathan et al. 2017). The spikelets vary from green to brown to purple and are positioned on one side or all around the rachis of the raceme. Spikelets are two-flowered, awnless or awned, and consist of red or green awns on short, rough pedicels supported by two glumes (Sood et al. 2015).

The flower is having lower floret with five-veined sterile lemma and tiny palea whereas the upper floret is bisexual and consists of fertile lemma which is plano-convex, elliptic margins are enrolled below over palea with apex of palea not enclosed (Gupta et al. 2010). The surface texture of palea is comparable to that of a fertile lemma (Napper 1965). The superior ovary features two distinct styles and a plumose stigma, whereas there are three stamens (Gupta et al. 2011). The grain is 1–2 mm broad and 2–3 mm long, and it is encased in a palea and lemma that are both hardened and white-shiny.

Flowering is in basipetal order, where the arrangement of flowers begins at the top of the inflorescence and progresses downward, takes approximately 10–15 days to complete. Anthesis takes place from 5 to 10 a.m., with the majority of the flowers open between 6 and 7 a.m. and close at 10 a.m. (Gupta et al. 2011). Flowering in an individual raceme originates from the periphery and progresses to the center. The flowers are hermaphrodite. Before the anthers dehisce, the stigmatic branches expand and the flower opens (Seetharam et al. 2003). Late-season florets are cleistogamous (not opening) (Sood et al. 2015). It is mainly self-pollinated and self-compatible, but few chances of outcrossing may occur owing to wind pollination (Sood et al. 2015) and the emergence of stigmatic branches prior to anther dehiscence allows for some cross-pollination (Seetharam et al. 2003). In both cultivated species, hot water treatment of inflorescence at 48 °C for 4–5 min was shown to be efficient to induce male sterility, particularly under hill conditions.

Compared to kodo millet and foxtail millet, barnyard millet seeds are less tough. A thorough investigation is needed to address the issue of seed dormancy, which is a key limiting factor in the production of tiny millets. According to Song et al. (2015), deep physiological dormancy in *E. crus-galli* grain is one of the most probable reasons for the long-term persistence of seed dormancy.

Furthermore, the innate dormancy of generated *Echinochloa* species hampers seed assessment and multiplication in germplasm conservation centers (Renganathan et al. 2020). Different dormancy-breaking techniques, including light, dark, cold, heat, or a mix of these, can be used (Renganathan et al. 2020). It has been demonstrated that application of 100 ppm of IAA (indoleacetic acid) to seedlings enhances the percentage of germination as well as germination speed and vigor.

Echinochloa species, classified as a short-day plant (Muldoon 1985), shows photoperiodism and the diverse photoperiod ranges from short days (8–13 h) to long days (16 h) generate various outcomes (Gupta et al. 2011). Such different performance with variable flowering time with hindered uniformity in grain yield has been observed in CO (Kv) 2 (Vanniarajan et al. 2018). To overcome this, MDU 1, a short-duration variety with stable yield performance, has been developed.

23.2.1 General Morphology of Barnyard Millet

Traits	Characteristics
Common name	Sawa millet/billion dollar grass/sava millet
Habitat	Annual crop, warmer region, Himalayan region in the North to Deccan plateau in the south

(continued)

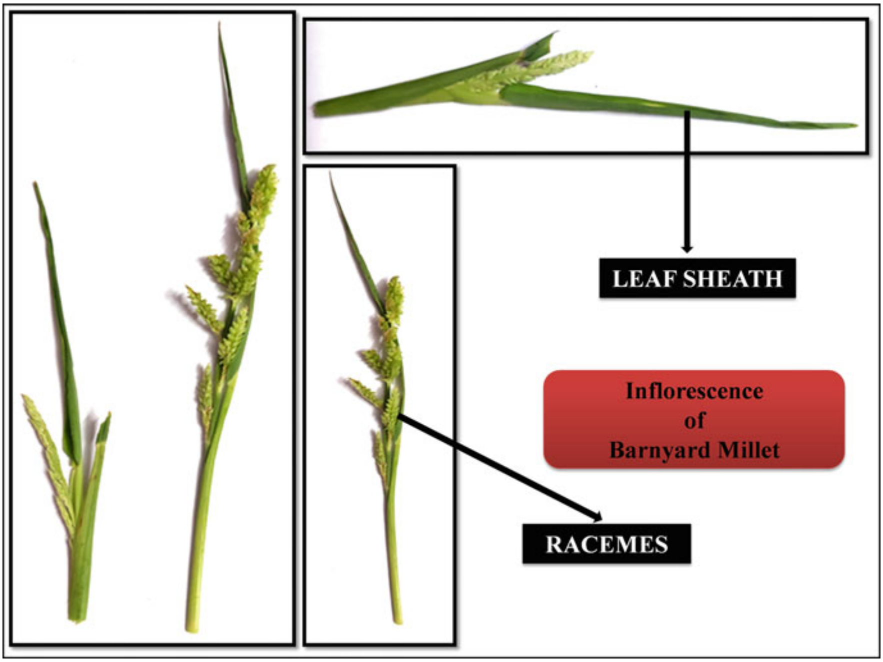

Fig. 23.1 Barnyard millet inflorescence

Traits	Characteristics
General morphology	Erect, 242 cm tall, leaf length 15–40 cm long and 1–2.5 cm wide, plants mostly green, moreover purple tings also present in both/either reproductive and vegetative parts. Culms being slender to robust, while leafblades are smooth and glaborous
Inflorescence morphology	Green to purple, erect and compact, 1–28 cm long inflorescence Racemes—numerous 20–70 in number, 1–3 cm long, rarely drooping and awnless
Spiklets on panicle	Spikelets on the rachis are compact and non-branched and are firmly grouped, 2–4 mm long, acute and awnless. It consists of 2 florets
Lemma and Palea	Lower floret: sterile lemma with tiny palea Upper floret: Bisexual, shiny lemma partially encloses with palea
Stamen and pistil	Stamen: 3 in number, fertile lemma and palea varying from white to dark purplish color Pistil: Bifid, plumose varying from white to dark purple
Caryopsis	Turgid and whitish
Seed dormancy	Physiological dormancy (seeds of both wild and cultivated species)
Seed shattering	High

See Figs. 23.1, 23.2, and 23.3.

Fig. 23.2 Different colors of Barnyard millet inflorescence

23.2.2 Anthesis and Pollination

The upper raceme of the flower opens first, and flowering occurs from the top of the inflorescence to the bottom. Under the conditions of the hills, the panicle emerges in 10–14 days and finishes flowering in 15–20 days. Six to eight days after flowering, the majority of the florets open (Bhinda et al. 2023). The majority of flower openings occur between 6 and 7 a.m., while flowers are open from 5 to 10 a.m. (Bhinda et al. 2023). Flowering within a single raceme first begins at both marginal ends, moves to the center, and finally finishes. Prior to the anthers dehiscing, the stigmatic branches extend and the flower develops (Seetharam et al. 2003). The blossom shuts in 30 min.

The total genome size is predicted to be 1.4 gigabases (Bennett et al. 1998, 2000). According to Schlegel (2010), the average diploid 2C DNA content of barnyard millet is 2.65–2.7 pg bot agr.

23.2.3 Germplasm Resources and Utilization

Genetic resources are the fundamental building blocks for genetic improvement in any crop. The preservation of the germplasm is utmost essential. Ex situ conservation is perhaps the most prevalent approach for conserving millet genetic resources.

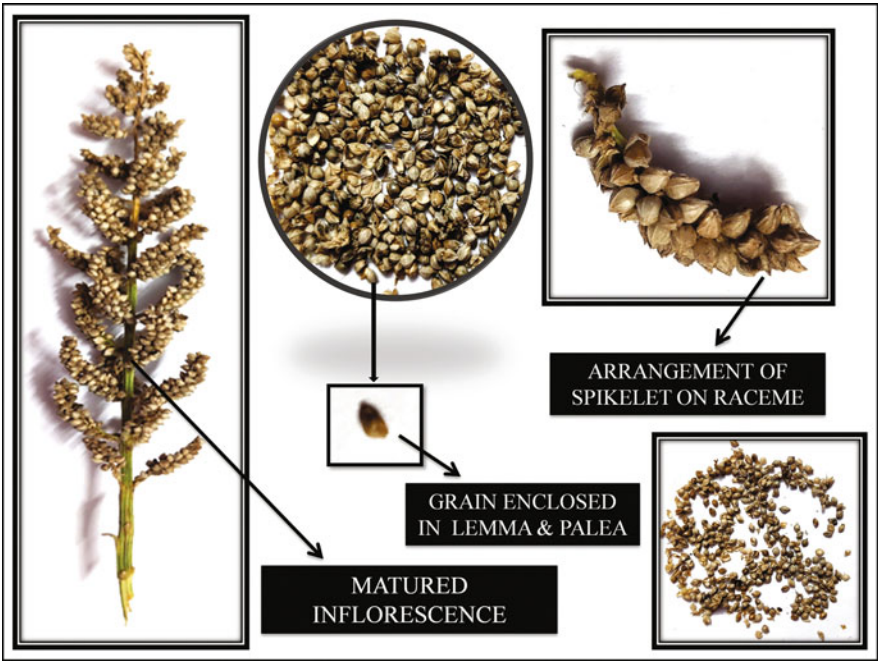

Fig. 23.3 Structure of matured barnyard millet inflorescence

Over 8000 barnyard millet accessions have been collected and conserved globally (Padulosi et al. 2009). The Consultative Group on International Agricultural Research (CGIAR) possesses the world's biggest ex-situ collection of barnyard millet, with 2365 accessions. The National Bureau of Plant Genetic Resources in India has the biggest barnyard millet collection, with 1677 accessions (Vetriventhan et al. 2020). The University of Agricultural Sciences in Bangalore, Karnataka, has 988 barnyard millet accessions as part of the All India Coordinated Small Millet Improvement Project. Barnyard millet has been represented by 749 active collections and 487 base collections at ICRISAT (Upadhyaya et al. 2008). Furthermore, the US Department of Agriculture lists 306 barnyard millet accessions in its National Plant Germplasm System (GRIN). Table 23.1 lists the major gene banks that are preserving barnyard millet.

For crop breeders to use germplasm, it must be characterized in addition to being collected, stored, and revived. It is crucial to collect barnyard millet before it goes extinct because accessions of the *laxa* race, which is unique to the Indian state of Sikkim, are underrepresented in ex-situ collections (Upadhyaya et al. 2014). The gathered materials' phenotypic analysis revealed that the barnyard millet germplasm is quite varied (Nirmalakumari and Vetriventhan 2009; Upadhyaya et al. 2016). Core collections encompassing 56 and 89 accessions, respectively, were produced by Gowda et al. (2009) and Upadhyaya et al. (2014) for the best and most accurate use of diversity for agronomic and nutritional development.

Table 23.1 Status of some significant germplasm collection of barnyard millet

Institute	Location	Number of accessions Barnyard millet
Department of Genetic Resources, National Institute of Agrobiological Sciences	Kannondai, Japan	3671 (3603 cultivated; 68 wild)
National Bureau of Plant Genetic Resources	Delhi, India	1888
Indian Institute of Millet Research	Hyderabad	1561
All India Coordinated Small Millets Improvement Project, University of Agricultural Sciences	Bengaluru, India	985
International Crops Research Institute for the Semi-Arid Tropics	Patencheru (Hyderabad), India	749
Institute of Crop Science, Chinese Academy of Agricultural Sciences	China	717
National Centre for Genetic Resources Conservation	Fort Collins, Colorado, USA	306
North Central Regional Plant Introduction Station, Ames	USA	304
Vivekananda Parvatiya Krishi Anusandhan Sansthan	Almora	300
USDA Agricultural Research Service, Washington	USA	232
National Gene Bank of Kenya, Crop Plant Genetic Resources Centre	Muguga, Kenya	208 (192 cultivated; 16 wild)
International Livestock Research Institute, Addis Ababa	Ethiopia	92
Tamil Nadu Agricultural University	Coimbatore, India	–
Australian Plant Genetic Resource Information Service	Biloela, Australia	66
Plant Germplasm Institute, Kyoto University	Japan	65
Plant Genetic Resources Program, Islamabad	Pakistan	50
Svalbard Gene Bank, Spitsbergen	Norway	44
Millennium Seed Bank Project, Seed Conservation Department, Royal Botanic Gardens, London	United Kingdom	44
Leibniz Institute of Plant Genetics and Crop Plant Research, Gatersleben	Germany	36

Source: http://apps3.fao.org/wiews/germplasm_report.jsp?

Halaswamy et al. (2001) selected and characterized promising accessions for increased plant height (seven accessions), larger number of basal tillers (nine accessions), taller inflorescence (10 accessions), and early flowering (27 accessions). Nirmalakumari and Vetriventhan (2009) discovered two new lines, IEC 566 and IEC 566/2, that vary from cultivated varieties in various ways, including the generation of numerous pollen grains and flowers which remain open for a long period with the stigma projecting fully so as to allow emasculation and pollination. The identification of Japanese barnyard millet cultivar PRJ 1 (2003) from Uttarakhand hills, a direct selection from ICRISAT germplasm, is believed to have the greatest influence on barnyard millet germplasm utilization in India (Gomashe 2017). PRJ 1 produced 40% more than the Indian barnyard millet control genotypes (Upadhyaya et al. 2008). In general, Japanese barnyard millet yields more than Indian barnyard millet in the hills; but, if sown late in the hills, the Japanese barnyard millet crop fails totally, whereas Indian barnyard millet yields some even under late-sown conditions. Similarly, an easy dehulling accession B29, found in Uttarakhand hills accessions and registered with NBPGR under the number INGR09023, had a 40% and 140% greater dehulled grain recovery than the control varieties VL 172 and PRJ 1, respectively (Gupta et al. 2009). GP 70 A, GP 90 A, GP 110, GP 117, and PRJ 1 are barnyard millet germplasm accessions exhibiting tolerance to grain smut. IIMR, Hyderabad (2016) analyzed 146 barnyard millet accessions and observed a greater variability in grain production and yield contributing factors, leading to the discovery of 18 potential barnyard millet breeding accessions.

Recently, MDU 1, a short-duration (<100 days), high-yielding barnyard millet with pyramidal inflorescence and incurved compact raceme has been developed at TNAU that yields on an average 1700 kg/ha and 2500 kg/ha grain under rain-fed and irrigated condition respectively (Nirmalakumari et al. 2009). Apart from that, the variety exhibits greater iron content (16 mg/100 g) in the grains with good milling and cooking quality.

There is a requirement for a detailed description and evaluation of the available germplasm preserved in national gene banks, particularly the wild weedy species, in barnyard millet. It aids in identifying trait-specific germplasm, especially for grain production, insect pest and disease resistance, and quality characteristics, which may then be utilized in broadening the crop's genetic basis.

Over several years, 729 accessions of *E. frumentacea* (Roxb.) Link. were examined for yield and yield characteristics in Barnyard millet, and a core set of 50 accessions was created (Gowda et al. 2009) (Table 23.2).

In barnyard millet, gene flow mainly occurs through intraspecific hybridization. Maun and Barrett (1986) reported a high degree of self-fertilization among barnyard millet population. The information on interspecific hybridization in case of barnyard millet is very meager. Inter-specific hybrids for early maturity and high yields were developed using *E. frumentacea* (early maturing) and *E. esculenta* (high yielding) but were found sterile both ways (Mehta et al. 2005). Similarly, sterile hybrids were obtained when inter-specific hybridization was carried out between Japanese and Indian Barnyard millet for grain smut resistance (Sood et al. 2014).

In India, Uttarakhand and Tamil Nadu are the major states involved in the breeding of barnyard millet, and most of the varieties have been developed through mass selection and pure-line selection followed by hybridization and pedigree selection. In *Echinocholoa*, gamma radiation has been used to develop mutants for various traits, including grain yield, plant height, tillers per plant, and head length and waxiness (Kumar et al. 2016).

Table 23.2 Trait-specific barnyard millet germplasm identified in the Indian program

Traits	Promising genotypes	Reference
Grain smut, head smut, sheath blight	HCBM 1016/HCBM 1018, HCBM1019, HCBM1020	NBPGR Annual Report (2012)
Grain smut	TNAU 25, TNAU 63, VL 10, PRJ1, PRB 903, DHBMV 56-6, DHBMV93-3, RBM 82, RBM 45, RBM 78, RBM 85	NBPGR Annual Report (2012; 2013)
Shoot fly	VL 207, VL 172, TNAU 151, TNAU 155, KOPBM 46	NBPGR Annual Report (2012)
Days to 50% flowering	IEC 336, IEC 343, IEC 344, IEC 330, IEC 217, JEC 340 and JEC 338, IC257799	NBPGR Annual Report (1986; 1987)
Days to maturity	IEC 157, IEC 159, IEC 71, IEC 78, IEC 257, IEC 271, IEC 158, IEC 156, IEC 282, IC426595, IC436926, IC426594, IC257799	NBPGR Annual Report (2011–2012)
Basal tillers	IC257799, IC24848, VL 29, IC52701, IC338896	NBPGR Annual Report (2011)
Length of inflorescence	IC426595, IC97034, VL. 29, IC97031	NBPGR Annual Report (2011)
Width of inflorescence	IC426594	NBPGR Annual Report (2011)
1000 seed weight	IC326725, KLI	NBPGR Annual Report (2011)
Yield per plant	IC97034, VL 29 IC338960, IC97031	NBPGR Annual Report (2011)
Ear head length	IC548696, IC548635, IC548697	NBPGR Annual Report (2011)
Plant height	IC548681, IC548696, IC548658	NBPGR Annual Report (2011)
100 seed weight	IC548641, IC538089, IC548697	NBPGR Annual Report (2011)

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