5

Breeding Strategies in Foxtail Millet

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Abstract

Foxtail millet is a highly self-pollinated crop, and the small delicate flowers make hybridization and crossing difficult. Progress in crop improvement of foxtail millet has been achieved chiefly through pedigree selection in many parts of the globe. China has been pioneering in developing male sterile lines and yield gains through heterosis. Many male sterile systems have been developed in China and are used for commercial production. Methods of crossing through physical and chemical treatments are in their infancy. In order to realize a yield benefit in this nutritionally rich and highly climate-resilient crop, recombination breeding and hybrid technology need to be developed.

5.1 Introduction

Foxtail millet is a diploid ($2n = 18$), C4 panicoid crop. Cultivation of foxtail millet is now limited to certain pockets, and in several areas it has been replaced by other crops with irrigation. Its superior nutritional quality coupled with its low requirement for water, makes it a climate-resilient crop suitable for cultivation under dry land agricultural systems (Muthamilarasan and Prasad 2015; Muthamilarasan et al. 2016). It has a small genome, and its use as a model crop for bioenergy has created a momentum with more groups working than before (Muthamilarasan and Prasad 2015). However, unless yield gains are realized it is difficult for farmers to afford to grow this crop. Yield gains through heterosis and recombination have progressed in China much more than other parts of the globe. In other parts of the world the crop improvement in foxtail millet has been achieved to a larger extent by selection and through recombination breeding to a smaller extent. Floral morphology and flowering behavior of this crop make it difficult to take up crosses between the desired parents. Thus, we have seen many research publications to date on developing methods for crossing in foxtail millet. In this chapter we discuss the floral biology, crossing

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methods, and development of cytoplasmic male sterile (CMS) lines.

5.2 Floral Biology

Floral morphology and anthesis behavior make foxtail millet one of the most difficult species to cross-pollinate (Baltensperger 1996). A floral description of foxtail millet has been presented by Gupta et al. (2011). It is mostly a self-pollinated crop with cross-pollination averaging about 1.4–4% (Li et al. 1935; Till-Bottraud et al. 1992). The inflorescence of foxtail millet is a terminal spike that consists of the main stalk and short side branches (Fig. 5.1a). Branches bear spikes and bristles (Fig. 5.1b, c). Bristles generally terminate inflorescence axes and appear paired with spikelets (Fig. 5.1d, e). There are up to eight orders of branching in foxtail millet, each branch initiating meristems which differentiate into spikelets or bristles (Doust et al. 2005). Each spikelet contains two florets embraced by a pair of glumes (Fig. 5.1f). The lower floret is sterile whereas the upper one is fertile or bisexual with three stamens and a long oval, smooth ovary with two long styles that terminate in a brush-like stigma (Fig. 5.1g) (Hector 1936; Nirmalakumari and Vetriventhan 2010). The anthers are yellow or white in color. Flowering in foxtail millet starts from the top of the main spike and proceeds downward. It takes

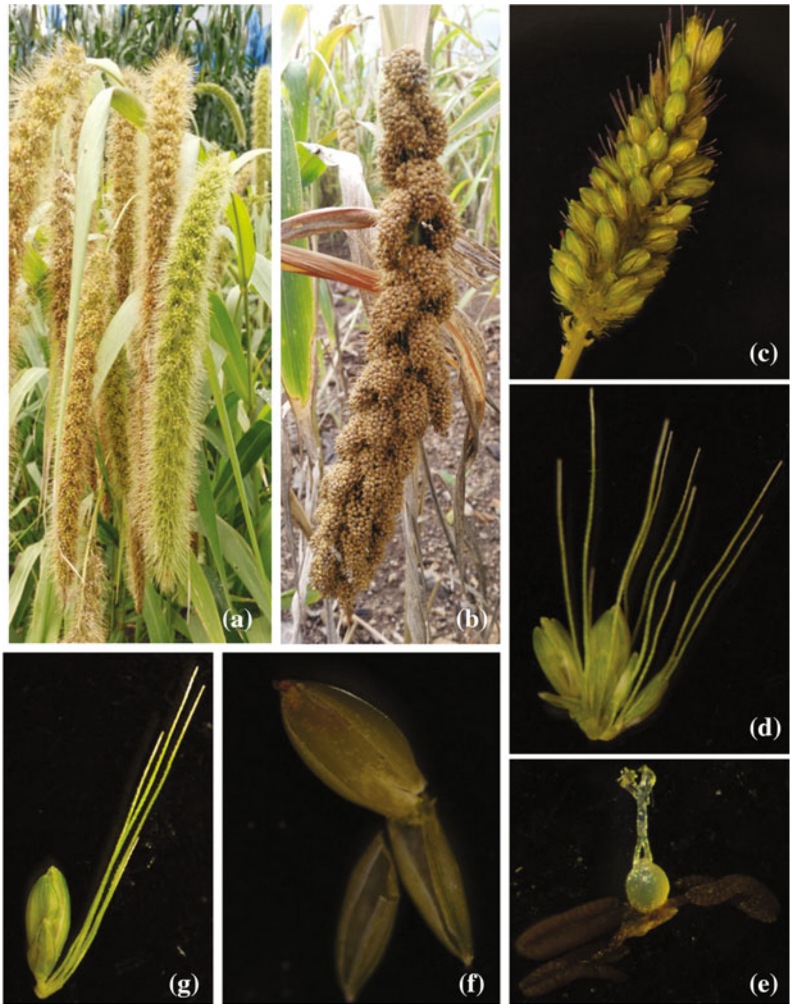

Fig. 5.1 Floral biology of foxtail millet

8–16 days for an ear head to complete flowering. A single floret remains open for about 30 min, and it takes around 80 min for complete blooming to take place. The rates of both these parameters are affected by temperature and atmospheric humidity (Heh et al. 1937). During pollination, stigmatic branches emerge first, followed by the emergence of anthers through the slit between palea. Once the anthers are fully extruded outside the glumes, they shed pollen. After dehiscence the glumes close, leaving the shrivelled anthers and tips of stigmas outside. Anthesis in foxtail millet takes place near midnight and between 8 and 10 a.m. A maximum number of florets open on the 6th day of flowering (Sundararaj and Thulasidas 1976). The flowering pattern is influenced by temperature and varies between crop seasons. We found that crops sown in the post-rainy season (*rabi*) flower till 9 a.m. in the cool winter days of December and January. High pollen fertility was observed during this period. This is best time for taking up crosses in India at Hyderabad.

Green foxtail millet (*Setaria viridis*) is a close relative of foxtail millet. It has a short life cycle, small plant stature, and a high number of seed set, and is a model species for the study of C4 plants. Studies have been extensively carried out on understanding its floral biology in this species. Using a time-lapse digital recording technique, Rizal et al. (2013) found that flowering in *Setaria* was triggered by the darkness of the night and a temperature lower than 35 °C. The anthesis of all the spikelets in a panicle took up to three nights flowering from 9:30 p.m. to 10:00 a.m. Flowering started from the tip and proceeded to the middle in the first night. Each spikelet was found to have three phases of anthesis during which pollination occurs. A spikelet generally remained open for less than 3 h. The pollination time for each spikelet was less than 60 min. All spikelets on the cluster did not flower at the same time. The anthers elongated taller than the stigma, and after a rapid desiccation they collapsed, mostly on the stigma. Once the spikelets are closed, vestiges of the anthers and stigma remain outside. The remains of the anthers which turn from yellow to brown are a sign that the spikelets have opened and fertilized. Information from studies on green foxtail millet would enable the geneticists and plant breeders to develop efficient crossing techniques in *Setaria italica*.

5.3 Crop Improvement

Wide genetic diversity is available in the germplasm resources for agronomically important traits, but has remained unexplored (Upadhyaya et al. 2015). Hybridization and selection are primary means of availing genetic variability for cultivar development in any crop species. A very low degree of natural cross-pollination was observed in foxtail millet. The International Crops Research Institute for the Semi-Arid Tropics genebank is presently holding 1,474 cultivated germplasm accessions from 23 countries. To facilitate the breeding efforts, a core collection (10% of the entire collection) was characterized using the taxonomic and qualitative traits. The germplasm accessions were stratified into three taxonomic races (Indica, Maxima, and Moharia) (Upadhyaya et al. 2009). Vetriventhan (2011) identified trait-specific accessions based on their performance in three environments in foxtail millet for economically important traits such as yield and traits contributing to yield (15 accessions for each trait) to be used in recombination breeding to develop high-yielding cultivars. Population diversity was analyzed using SSR (simple sequence repeats) markers and was estimated to be having low linkage disequilibrium (LD), suggesting the possibility of high-resolution association mapping (Wang et al. 2013; Jia et al. 2013; Zhang et al. 2014). This produces ready-to-use information for foxtail millet breeders.

Foxtail millet genotypes under cultivation in India, USA, and many other places, barring China, are mostly selections from landraces, and efforts to avail recombination breeding and hybrid programs are very few. Primarily it is because of the difficulty in making crosses, the florets are very small in size to handle, and flowering takes place in the early hours of the day, making it difficult to work. High heterosis for grain yield and other important agronomic traits was observed in F_1, and the genes controlling grain yield, plant height, and spike length are tightly linked (Siles et al. 2004). Based on the high degree of heterosis observed in an F_2 generation, the authors suggested an alternative of growing F_2 generations or other types of populations with a relatively high percentage of heterozygous genotypes to provide significant yield benefits over non-hybrid varieties. Radiation and chemical-induced mutations have also been used in foxtail millet breeding to create novel types, such as dwarf lines. Single plants were selected from landraces, improved varieties of farmers, and the progeny were tested. Superior progenies, mostly for earliness, pest and disease resistance, and grain yield, were evaluated in multi-location trials, and released as varieties. Genetics of several agronomic characters has been studied and consolidated for ready use in plant breeding programs (Hariprasanna 2017). Pure line selection has resulted in the development and release of a maximum number of foxtail millet varieties in India. Hybridization-based pedigree selection is the main breeding strategy in China. Later, the introduction of male sterility and heterosis contributed to the quantum jump in the yields of foxtail millet in China.

Exploitation of heterosis in crops is the most important means of crop improvement. Heterotic vigor obtained from the cross-fertilization of genetically different parental lines is one of the most important means of improving yield parameters and quality traits, in addition to developing tolerance to stresses in crop plants. Heterosis and hybrid vigor have been demonstrated in China (Diao and Jia 2017). Siles et al. (2004) reported a high level of heterosis for grain yield among intervarietal crosses. The authors suggested that the crosses between highly heterozygous parents provide significant yield gains. China has attained the yield gains through commercial hybrids that were produced based on the male sterile line. Male sterility such as genetic, cytoplasmic, photosensitive or thermosensitive can all be used to make crosses between diverse parents and exploit the recombination or heterosis. Male sterility can be used for the production of commercial hybrids on a large scale and also to recombine diverse parents for genetic gains. All the above types of male sterile lines are generated and used in China, but other parts of the world do not have them. Access to these lines from one country to another is difficult because of intellectual property rights on material transfer. In India, the crop improvement in foxtail millet was limited to pure-line selection, and efforts toward recombination breeding are on increasing trend (Hariprasanna 2017). In the USA the breeding program is limited and most of the lines cultivated today are selections from landraces rather than designed crosses (Siles et al. 2001).

5.4 Crossing Methods

Genetic improvement in this crop suffers because of the absence of an efficient crossing technique. Taking up crosses in foxtail millet is difficult, and hence not exploited to its full potential. Floral morphology and anthesis behavior make foxtail millet [*S. italica* (L.) Beauv.] one of the most difficult species to cross-pollinate (Baltensperger 1996). The minuteness of the flowers, the delicate and environment-dependent process of anthesis, and timing of anthesis make hybridization a tedious task in foxtail millet. Siles et al. (2001) devised a crossing method in which an average 75% seed set and more than 90% true hybrid seed was accomplished by emasculating a high number of florets as optimized on the second day, starting from the opening of flowers. In some of the earliest attempts to enhance the chances of natural cross-pollination, panicles of selected plants were enclosed in a parchment bag before flowering (contact method) (Ayyangar 1934), resulting in a low frequency (1.5%) of true hybrids (Mahishi et al. 1982). The technique of controlled hybridization with the removal of anthers and artificial pollination, although very difficult because of the small flower, started yielding improved cultivars by the mid-1990s.

During emasculation, the bristles of the female and the male parents are excised gently with a pair of scissors. After the bristles are excised, emasculation has to be done when the first anther had just emerged and before the pollen sacs burst. Anthers are to be removed by gently inserting forceps at each side of the palea and pushing the anther out quickly. Each emasculated flower is then immediately marked with a fine point black or blue permanent marker so that emasculated flowers can be identified easily. The male and the female spikelets are tied together or enclosed in a bag. The bag has to be tapped in the early hours of the day for 3 days more. Later the male spikelet is removed, and the female is bagged separately. It is critical to watch and remove the anthers after emergence but before the burst. Jiang et al. (2013) provided a video on the methods of crossing *S. viridis*, which is very useful for setting up a crossing program.

Artificial emasculation is done through a spray or dip in hot water, cold water, and chemical agents. Rizal et al. (2013) found that a floral dip in hot water at 48 °C for 3–6 min was useful to recover three to five outcross progeny per panicle in *S. viridis*. Chemical spray with 500 µM maleic hydrazide was effective without loss of stigma receptivity (Rizal et al. 2015). The authors provided a detailed description of the emasculation procedure, which can be readily followed. In our study with *S. italica* we completely remove the bristles with scissors. Spikelets are removed carefully at random at the base, leaving a few (can be 10–30) florets. Because of this, all the intact spikelets are separated and exposed. Top and bottom spikelets are also removed in the panicle. Panicles for crossing are covered by a small parchment cover, taking care not to break them. We also observed that floral dip gives better results than floral sprays. For crossing, pollen from the male parent was sprayed on the emasculated panicle for crossing (Rizal et al. 2015). We bring the male and female parents together, gently tie the emasculated panicle and pollen shedding panicle with a thread so that they are intact, and later cover them with a paper bag. This ensures pollination if the flowering takes place at odd hours. *S. italica* is the cultivated crop species and has been improved for grain and related traits. Hence it contains long panicles with many secondary branches and more florets (Fig. 5.1b). Thus, emasculation in *S. italica* is more complicated. Flowering time varies with seasons between midnight in summer and the early hours in winter. The crossing programs can be taken up on a large scale during the winter months. Spray of SQ1, a chemical hybridization agent (CHA) at the early protogyny stage at a concentration of 5 kg/ha was effective in the induction of male sterility in the field (Yu-Long et al. 2011; Zhang et al. 2017). This can be used for hybrid seed production on a commercial scale.

5.5 Male Sterility

China has been pioneering the development of male sterile lines of foxtail millet. Utilization of heterosis has gained momentum in China and various male sterile lines have been identified such as (1) genic highly male-sterility lines (GMS) (Hu et al. 1986), (2) photo-(thermo-) sensitive nuclear lines (PMS or TMS) (Cui et al. 1979; Wang et al. 1993, 2002; Zhao et al. 1996; Hao et al. 2009), (3) cytoplasmic male sterility (CMS) (Zhu et al. 1991), (4) cytoplasmic-nuclear male sterile type (Zhi et al. 2007), and (5) partial genetic male sterile line (PAGMS). Research using heterosis for foxtail millet began in the 1960s with the development of male sterile lines by various approaches (Diao and Jia 2017). Production of foxtail millet in China has passed through pedigree selection, development of male sterile lines, and commercialization of hybrids through the use of a partial male sterile line. Many GMS lines were developed through hybridization between landraces and crossing foxtail millet with other *Setaria* species (Cui et al. 1979; Zhu et al. 1991).

A GMS line, Ch78182, was derived from the cross between Australian and Tulufan races and a complete (100%) restorer line, 181–5 and was identified for seed production (Hu et al. 1986). Ch__ genotype is a dominant male sterile gene, and fertility in restorer line is controlled by the epistatic interaction of Ms__ and Rf__ genes. Thus, the male sterility is suppressed completely by the Rf__ gene. In the line Ch78182, sterility was found to be because of the lack of anther dehiscence, though the pollen grain development was complete. Thus, occasional fertility was observed in this line and could not be used for commercial seed production.

Photoperiod-sensitive male sterility (PMS) is a useful genetic tool for the development of two-line hybrids in self-pollinated crops. In this system, the plant fertility/sterility is regulated by the photoperiod, and the PMS gene(s) cause(s) male sterility under long daylight (LD) or short daylight (SD) conditions and results in fertility under an SD or an LD condition. The first PMS line was reported in foxtail millet in 1996, line 821 (Zhao et al. 1996). The PMS line is maintained and multiplied by self-pollination under SD conditions, and hybrid F_1 seeds can be produced through outcrossing with restorer lines under LD conditions. The PMS line had the advantage of obtaining a high purity of F_1 seeds, and line 821 had the disadvantage that it required a critical photoperiod for hybrid production. This lacuna was overcome by the development of a PMS line, JG1S, which was completely sterile under natural LD conditions and fertile under SD conditions. The line was studied in depth and the inheritance pattern analyzed a few years later (Yuan et al. 2008). A PMS line, JG1S, was identified that was completely sterile under long daylight conditions (14.5 h/day) and partially sterile under short daylight conditions (10 h/day) (Yuan et al. 2008).

A highly nuclear-male-sterile line of foxtail millet with the recessive nuclear sterile gene, with 100% of the sterility percentage, and 95% of the sterility degree rate was crossed with a superior restorer line, and six varieties and a series of variant generation materials with favourable characters were bred from the cross (Wang et al. 1993). A highly genic male sterile line Gao146A was identified by Wang et al. (2013), which showed 95% sterile rate and was not sensitive to light and temperature. F_1 generation was fertile, and the segregation ratio of fertility to sterility was 3:1 in F_2 generation, indicating that a single recessive gene controlled the trait. Using F_2 population derived from the cross Gao146A/K103, one gene controlling the highly male sterility, tentatively named *ms1*, was mapped on chromosome VI using SSR markers (Wang et al. 2013). Heterosis has also been used in developing hybrid cultivars. Zhangzagu5, a hybrid cultivar, was released from Zhangjiakou Academy of Agricultural Sciences, Hebei Province, China, and yielded 12,159 kg/ha vs conventional cultivars ranging from 4,500 to 6,000 kg/ha in 2007 (Liu et al. 2014).

CMS is maternally inherited and can be transferred to different genetic backgrounds through repeated backcrossing. Sterility of the lines is maintained by crossing the MS line (A line) to the complimentary fertile (B) line. Suitable restorer lines that restore 100% fertility and show hybrid vigor are used as male parents for commercial hybrid seed production. These CMS lines are developed by different methods. One of them is through spontaneous mutation and/or interracial crosses between geographically distant species. In foxtail millet CMS line derived thus could not lead to true CMS, which was a discouraging factor for commercial seed production. By distant hybridization of *Setaria verticillata* with foxtail millet, a CMS line was developed (Zhu et al. 1991). However, it was not used for hybrid seed production. A significant step in heterosis breeding in foxtail millet was the development of Suanxi 28, a partial male sterile line developed from a spontaneous mutant from the landrace Suanpibai, which led to a new hybrid seed production system (Diao 2017). This line was used for hybrid seed production and was maintained through selfing (3–5% seed set). Thus, a two-line system of hybrids was developed in China with the help of Suanxi 28. Despite the development of several male sterile lines, PAGMS is used successfully in hybrid production (Diao and Jia 2017). New hybrid cultivars developed through the two-line system using PAGMS showed higher yields than conventional varieties. This system prevailed in China for hybrid seed production for many years, even though other types of male sterile lines have been explored and developed.

Interspecific crosses between foxtail millet and green foxtail have resulted in 65–70% sterility, which has been utilized for developing male sterile lines. However, most of the Chinese spring foxtail millet male sterile lines were derived from ‘Chang 10A’, whose cytoplasm was contributed by ‘Qinyuanmujizui’ (Liu et al. 2014; Wang et al. 1998). The summer foxtail millet male sterile lines were derived from ‘Huangmi 1A’ with the cytoplasm from ‘Dahuanggu’ (Liu et al. 1996, 2006). CMS is inherited maternally, and hence all the hybrid plants carry the same cytoplasm; it threatens the vulnerability of all the female parental lines to CMS-related diseases and disasters. The narrow genetic base of CMS in China was confirmed through analysis using mtDNA-specific primers (Liu et al. 2014). Because of the maternal inheritance of cytoplasm, using a single source of cytoplasm in male sterile lines makes hybrid cultivars vulnerable to infection by cytoplasm-related diseases, leading to epidemics. Thus, there is always interest in searching for novel sources of male sterile lines.

5.6 Interspecific Crosses

The earliest efforts in wide hybridization were successful with *S. viridis* and *Setaria faberi* (Li et al. 1944). The wild green foxtail, *S. viridis*, and the cultivated foxtail millet, *S. italica*, are compatible for crossing at very low rates (Till-Bottraud et al. 1992). A wild relative of cultivated foxtail millet, *S. viridis*, is a source of important traits. These two are compatible, and the genetic background of cultivated line can be easily restored in two backcrosses and the weedy traits in the inter-specific cross derivatives can be eliminated (Naciri et al. 1992; Zangre and Darmency 1993). Darmency et al. (1987) could obtain a twofold increase in seed weight in the F_1 interspecific hybrid after colchicine-induced tetraploidization of F_1. Although the option is promising, it has practical difficulties. From the hybridization of *S. italica* with its wild relative *S. verticillata* (a tetraploid), a CMS line was developed (Zhu et al. 1991). Sterile F_1 plants were backcrossed to *S. italica* in three backcrosses. The Chinese CMS was derived with great difficulty from repeated crosses with *S. verticillata* and hence named as VeCMS. Despite the difficulties in crossing, primary trisomics of foxtail were constituted by inducing autotetraploids in tissue culture and crossing them to the diploid parent (Wang et al. 1999).

5.7 Conclusion

Foxtail millet is nutritionally rich, and entrepreneurship in the nutraceutical industry is picking up globally because of its health benefits. Consistent and constant supply of grain for various end uses in terms of quantity and quality is the prerequisite to meet industrial demands, and it can be met only through increasing yield. Because heterosis, in terms of yield gain, is promising, two areas need to be promoted: (1) recombination breeding and release of high yielding varieties and (2) hybrids for heterosis on a commercial scale. This would contribute to the nutritional security and health security of humans and animals.

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