Foxtail Millet: An Introduction

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Abstract

Foxtail millet (*Setaria italica* L.) is a versatile crop known for being genetically closely related to biofuel grasses, for its C_4 photosynthesis, and for its tolerance to abiotic stresses. These attributes have made this crop a model system and, in view of this, the genome of foxtail millet has been sequenced. Among millets, foxtail millet is the only crop possessing rich genetic and genomic resources, and globally it is the second most cultivated millet next to pearl millet. In the context of its importance in agronomic and research terms, the present chapter summarizes the origin, domestication, phylogeny, and agroeconomic importance of foxtail millet.

1.1 Introduction

The term 'millets' refers to a diverse group of annual cereal crops that characteristically produce small seeds. They include several food, fodder, and biofuel grasses, such as foxtail millet (*Setaria italica*), finger millet (*Elucine coracana*), pearl millet (*Pennisetum glaucum*), proso millet (*Panicum miliaceum*), kodo millet (*Paspalum scorbiculatum*), barnyard millet (*Echinocloa* sp.), etc. (Dwivedi et al. 2012). The major distinctive feature of the millets is their adaptability to cope with adverse agro-ecological conditions such as a semi-dry environment and nutritionally poor soil, the requirement of minimal inputs, and highly nutritious seed content (Lata et al. 2013). Millets require very little water for their cultivation—just around 25–30% of the annual rainfall required by crops such as rice and sugarcane. Thus, millets do not require irrigation and power for their production. In addition, millets also not require any synthetic fertilizers and are completely pest-free crop as none of the millets attracts any pests. Thus, the production of millets is very economical for farmers because of almost nil expenditure on irrigation, fertilizers, and pesticides. Importantly, seeds of most millets can be stored for longer period and are not affected by storage pests. Nutritionally, millets are several times superior to other cereal crops such as rice and wheat. They are rich in minerals

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including iron, calcium, potassium, zinc, and magnesium, vitamins, crude edible fibers, and are gluten-free with low glycemic index (GI). Millet consumption enables a reduced rate of glucose release over a longer duration of time and thus, because of the low GI, their routine ingestion decreases the risk of diabetes mellitus. Regardless of their excellent qualities, millet consumption as food is limited to conventional consumers, particularly rural populations, only in certain parts of the world. This is primarily because of the lack of awareness of their nutritious qualities among most people and the non-availability of customer friendly and ready-made millet-based products. In the past few years, global attention and efforts have been applied to millets to acquire expedient and value-added processed products in consumer markets.

Foxtail millet (*S. italica*) is an important crop used as a staple food in many parts of the world including arid and semi-arid areas of China, some part of India and Japan, and is grown for silage and hay in South and North America. Foxtail millet is commonly known in India as Kangni (Hindi), Kang (Gujrati), Navane (Kannada), Kaon dana (Bengali), Kavalai, and Tenai (Tamil), Kangam (Oriya); as Su, Xiaomi, Shao-mi, Kou wei tsao in China; Awa in Japan; Siberian millet and Dawa in Indonesia; Mohar in Russia; Millet des oiseaux and millet d'ItalieIt in France; Panico, Milho panico, and Milho panico de Itálica in Portugal; and Kimanga in Kenya. It is the second most cultivated millet after pearl millet. Worldwide, total millet production amounts to 29.8 million tonnes, the contribution of India being highest at 10.3 million tonnes (FAOSTAT data 2012; http://faostat.fao.org/). Because of its economic value the Joint Genome Institute (JGI) of the Department of Energy, USA and BGI (formerly Beijing Genome Initiative), China independently sequenced its genome, and the draft genome sequence was released in 2012. The most likely gene number for foxtail millet is around 24,000–29,000, which is in line with gene complements of other diploid grasses such as rice and sorghum (Bennetzen et al. 2012; Zhang et al. 2012). It has been recently identified as an excellent model crop for the study of genetic and molecular aspect of abiotic stress tolerance mechanism and physiology of C_4 photosynthesis process because of its small diploid genome (~515 Mb; $2n = 2x = 18$), self-pollinating, short growing cycle (50–80 days), small plant architecture and prolific seed production per plant, low repetitive DNA content (30%), and a highly conserved genome structure relative to the ancestral grass lineage such as switchgrass (*Panicum virgatum*), napiergrass (*Pennisetum purpureum*), and pearl millet (*P. glaucum*) (Sivaraman and Ranjekar 1984; Devos et al. 1998; Li and Brutnell 2011; Lata et al. 2013).

1.2 Taxonomy and Morphological Description

The genus *Setaria* has approximately 125 species widely distributed in warm and temperate parts of the world, and this includes *S. italica* (foxtail millet). This genus belongs to the subfamily Panicoideae and the tribe Paniceae. It contains grain, wild, and weed species with different breeding systems, life cycles, and ploidy levels (Lata et al. 2013). The genome of *S. italica* and *S. viridis* (green foxtail) is designated as AA genome with $2n = 2x = 18$ (Benabdelmouna et al. 2001a). Weedy tetraploid species *Setaria faberii* and *Setaria verticillata* have AABB genome, probably originating from a natural cross between *S. viridis* and another diploid species, *Setaria adhaerans* (Benabdelmouna et al. 2001a, b). *Setaria grisebachii* from Mexico has been identified as CC genome diploid species (Wang et al. 2009). *Setaria queenslandica* is the only autotetraploid (AAAA genome) species in genus *Setaria* whereas other polyploid species such as *Setaria pumila* and *Setaria pallide-fusca* do not contain the AA genome (Benabdelmouna et al. 2001a, b; Benabdelmouna and Darmency 2003). The taxonomic hierarchy of foxtail millet is as follows:

Kingdom: Plantae
Subkingdom: Tracheobionta

Superdivision: Spermatophyta
Division: Magnoliophyta
Class: Liliopsida
Subclass: Commelinidae
Order: Cyperales
Family: Poaceae
Genus: *Setaria*
Species: *italica*

Foxtail millet has a typical domesticated plant architectural form consisting of a single stalk or a few tillers, with large inflorescences that mature more or less at the same time. A fully-grown foxtail millet plant measures around 120–200 cm (3.9–6.6 ft) in height with slim, erect, and leafy stems (Fig. 1.1). The smooth and hairless leaves are arc-broad, whereas culms are erect and slender with hollow internodes. The stems are topped by a bristly panicle which is long (5–30 cm long) and mostly reddish or purplish (Fig. 1.1). They give the panicle the appearance of a fox's tail, which is the common name for cultivated millets belonging to the genus *Setaria*. The inflorescence is a contracted panicle, often nodding at the top; on account of its short branches, it resembles a spike. The spikelets are crowded and mixed with stiff bristles, the latter representing branches on which no spikelets are developed. Each spikelet contains only one flower with a yellow pistil. It has a short generation time (depending on the sample, approximately 5–8 weeks from planting to flowering, 8–15 weeks from planting to seed maturity) and can produce hundreds of seeds per inflorescence (Reddy et al. 2006).

A single inflorescence can produce hundreds of small convex seeds measuring about 2 mm in diameter, encased in a thin, papery hull which is easily removed in threshing. The color of the seeds varies greatly between varieties. The non-dormant seeds germinate readily in a glasshouse at densities up to 100 plants per square

Fig. 1.1 Foxtail millet plants cultivated in field condition. **a** Fully grown foxtail millet plants with inflorescence. **b** Bristle panicle. **c** Mature seeds

meter or in field conditions in temperate or tropical regions (Dekker 2003). It is a summer crop, typically planted in late spring. Harvesting for hay or silage can be carried out after 65–70 days (typical yield is 15,000–20,000 kg/ha of green matter or 3,000–4,000 kg/ha of hay), and for grain after 75–90 days (typical yield is 800–900 kg/ha of grain). Early maturity and excellent water use efficiency (WUE) make it suitable for cultivation in dry and arid regions.

1.3 Origin and Distribution

Foxtail millet is one of the oldest cultivated crops in the world, the earliest archaeo-botanical macro remains indicating its origin in Cishan and Peiligang ruins in Yellow River Valley in the northern province of China, approximately 7,400–7,900 years before present (BP) (Doust et al. 2009). Green foxtail (*S. viridis*) is the wild ancestral form of modern cultivated foxtail millet (*S. italica*) (Wang et al. 1995; Le Thierry d'Ennequin et al. 2000). A combination of foxtail millet and proso millet (*P. miliaceum*) cultivation was practised by the people in ancient China (Lu et al. 2009; Yang et al. 2012; Lata et al. 2013). It has been proposed by Vavilov (1926) that the prime center of evolution and diversification of foxtail millet was East Asia, specifically China and Japan (Fig. 1.2). Another school of thought hypothesized that foxtail millet was cultivated independently in arid and drier part of Europe and Middle East Asia approximately 4000 years BC as indicated by archaeological remains, ribosomal DNA, and isozyme and phenotypic variance (Jusuf and Pernes 1985; Hunt et al. 2008; Austin 2006). Neither cultivated nor wild samples of foxtail millet showed a clear differentiation of population structure, but both samples from China were the most genetically diverse, which supports the idea of the monophyletic origin of foxtail millet in China (Le Thierry d'Ennequin et al. 2000). Tillering and panicle shape were associated with domestication as indicated by quantitative trait loci (QTL mapping of candidate genes, whereas the origin of waxy phenotype in foxtail millet was associated with human selection (Doust et al. 2005).

Currently, foxtail millet is distributed in most of China, some parts of India, USA, Canada, the Korean Peninsula, Japan, Indonesia, Australia, and the northern part of Africa (Doust et al. 2009; Li and Brutnell 2011). In the United States, foxtail millet is primarily produced in the northern and western Great Plains, midwest,

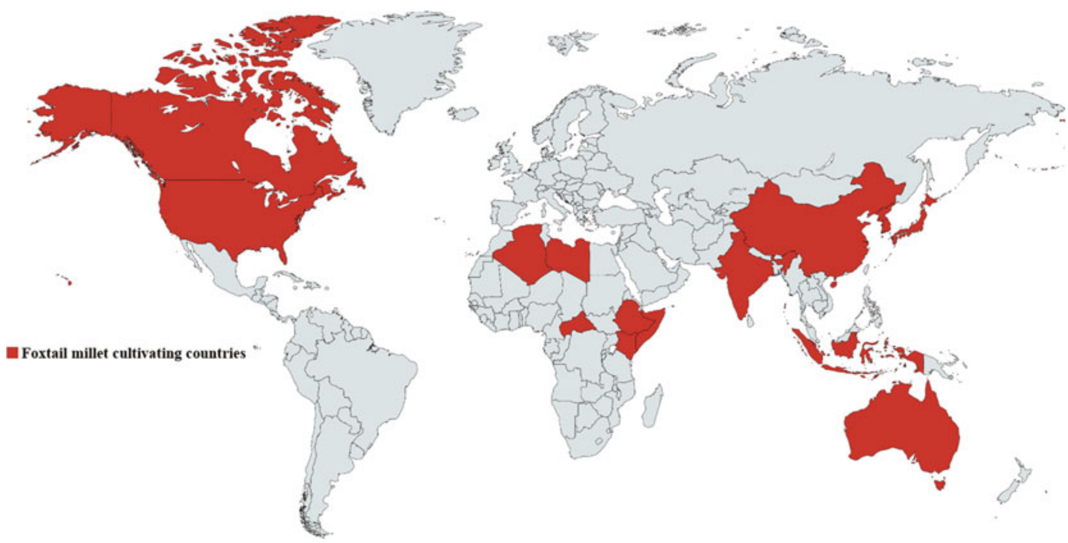

Fig. 1.2 Geographical distribution of foxtail millet cultivation. World map representing the regions highlighted in red where the foxtail millet cultivation is in practice

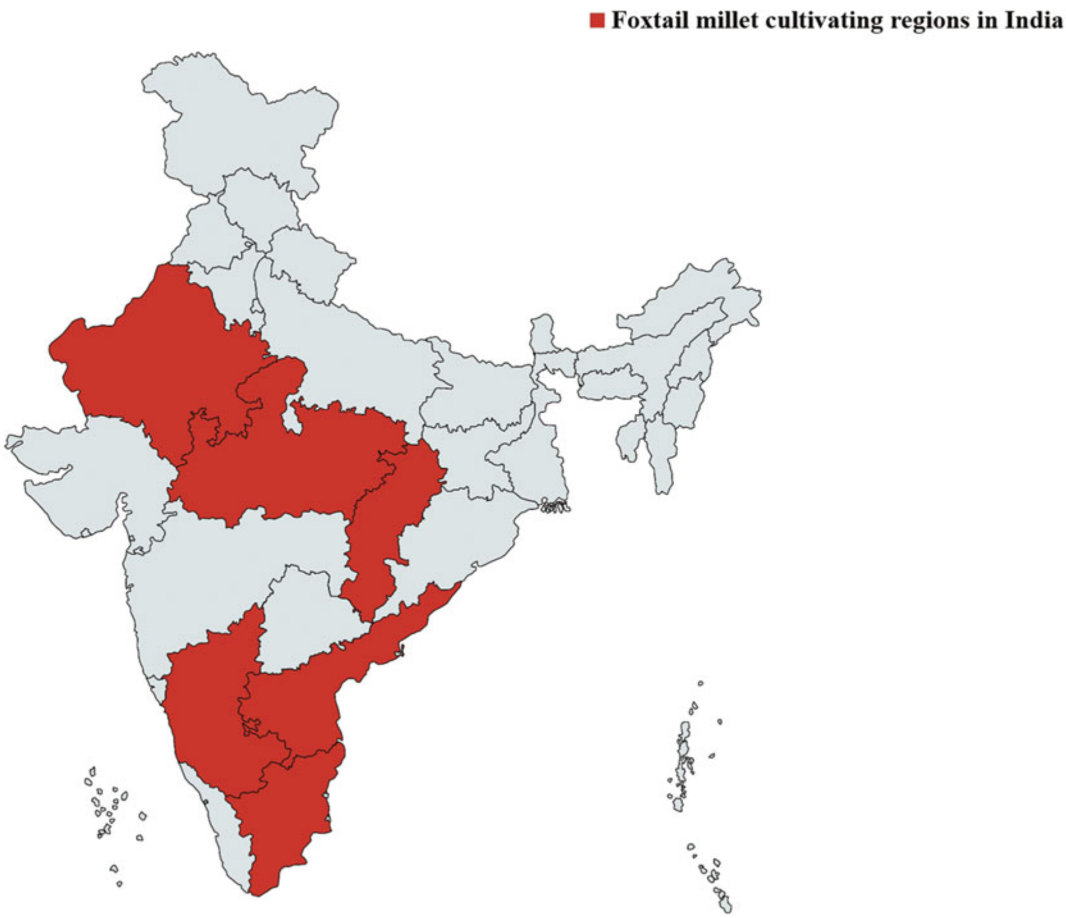

Fig. 1.3 Geographical distribution of foxtail millet cultivation in India. Map of India representing the regions highlighted in red where foxtail millet cultivation is practiced

Colorado, the Dakotas, Kansas, Wyoming, and Nebraska (Oelke et al. 1990; Baltensperger 1996). Foxtail millet can be found grown mainly for feed purposes in some part of southern Europe. In India, it is cultivated primarily in Karnataka, Andhra Pradesh, Rajasthan, Madhya Pradesh and Chhattisgarh, and Tamil Nadu (Fig. 1.3).

1.4 Phylogeny

An inclusive phylogenetic study based on nuclear as well as organellar DNA study revealed foxtail millet to be very closely related to green foxtail (Giussani et al. 2001; Doust et al. 2009). This also supports the hypothesis that, because of the course of evolution and domestication selection, foxtail millet has evolved from green foxtail (Wang et al. 1995; Le Thierry d'Ennequin et al. 2000; Doust et al. 2009). Both the species of genus *Setaria* are part of a larger monophyletic clade consisting of approximately 300 species, all with identical inflorescence (spikelets and bristles) features (Zuloaga et al. 2000). Foxtail millet morphologically differs from its wild ancestor green foxtail in its enlarged bristles with complex branching pattern, flowering synchrony, condensed axillary and basal vegetative branching, and loss of seed dormancy and disarticulation (Doust et al. 2004; Doebley et al. 2006; Lata et al. 2013). Furthermore, it is also closely related to several other biofuel crops such

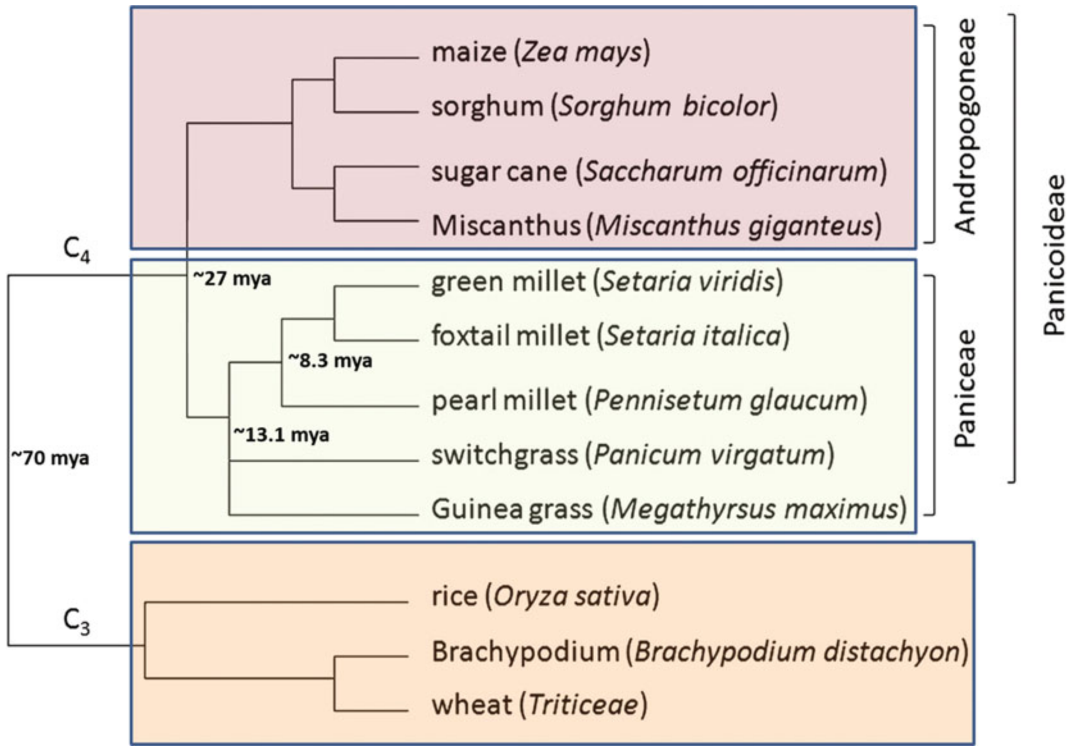

Fig. 1.4 Phylogenetic relationship of *Setaria italica* relative to selected important grass family members

as switchgrass, napier grass, and pearl millet at the genome level, and hence has been suggested to represent a relevant model for this class of crops (Doust et al. 2009; Lata et al. 2013). *Setaria* last shared a common ancestor with pearl millet ~8.3 million years ago and with switchgrass and proso millet ~13.1 million years ago (Vicentini et al. 2008). Later, it was separated from sorghum and maize ~27 million years ago. It was estimated that a whole genome duplication event had occurred to all members of the grass family ~70 million years ago, before the separation of *Setaria* from maize and sorghum (Fig. 1.4). There is highly conserved collinearity between genomic regions of *S. italica* and rice (71.8%), maize (86.7%), *Brachypodium* (61.5%), and sorghum (72.1%), which indicates some close evolutionary relationships between these grasses (Zhang et al. 2012).

1.5 Agro-Economic and Nutritional Importance

Being a C_4 photosynthetic crop, foxtail millet is naturally equipped with excellent WUE and nitrogen use efficiency, and, in addition, several morpho-physiological traits including dense and deep root systems, smaller leaf area, and thickening of cell walls which were thought to lead to durable tolerance to a range of abiotic stresses—mainly drought, heat, and salinity (Lata et al. 2013; Diao et al. 2014). In addition to that, the grains of foxtail millet require only 26% of their grain weight in water to germinate, whereas other major cereals such as rice, wheat, and maize require a minimum of 45% of their grain weight. Similarly, to produce 1 g dry biomass, foxtail millet requires only 257 g of water, which is the minimum among other cereals, as wheat and maize requires 470 and 510 g, respectively (Diao et al. 2014). These properties of foxtail millet demonstrate the important agronomical features and climate resilient characteristics.

Further investigation of genetics and genomics of abiotic stress mechanisms had revealed that foxtail millet has a novel gene as well as known stress-responsive genes which participate in stress tolerance (Muthamilarasan and Prasad 2015). Among abiotic stresses, heat, drought and salt stress are the instant impact of climate change and, in this regard, the research community is actively involved in understanding the genetics and genomics of crops tolerant to these stresses, with the goal of engineering these traits in stress-susceptible plants (Kole et al. 2015). Understanding the significance of foxtail millet as a model crop for abiotic stress biology, efforts have made to investigate the role(s) of several stress-responsive genes including *AP2/ERF* (Lata et al. 2011, 2014), *NAC* (Puranik et al. 2011, 2013), *WD40* (Mishra et al. 2012, 2014), C_2H_2 *zinc finger* (Muthamilarasan et al. 2014a), *MYB* (Muthamilarasan et al. 2014b), *DCL*, *AGO*, and *RDR* (Yadav et al. 2015), *WRKY* (Muthamilarasan et al. 2015), and *ADP-ribosylation factors* (Muthamilarasan et al. 2016b), *HSP* (Singh et al. 2016), and *SET* (Yadav et al. 2016) in response to several abiotic stresses.

Foxtail millet grain is rich in protein (14–16%), crude fat (6–8%), and iron along with zinc and calcium (Muthamilarasan and Prasad 2015; Muthamilarasan et al. 2016a). Not only is the biological value of digestible protein higher than rice and wheat; seven of the eight essential amino acids, which cannot be synthesized by the human body, are higher in foxtail millet (Zhang et al. 2007). A grain of foxtail millet contains approximately 2.5 times the edible fiber found in rice, and is thus a promising source of edible fiber, which is important for intestine and stomach health (Liang et al. 2010). Foxtail millet bran contains 8–10% crude oil and is rich in linoleic (66.5%) and oleic (13.0%) acids (Liang et al. 2010). Through the long cultivation and utilization as food, were fashioned using foxtail millet seeds. In China its flour is used to make bread, chapattis, pancakes, and snacks. Steamed bread made from composite flour some different methods of consumption containing foxtail millet, wheat, and soybean has gained prominence in Northern China (Diao et al. 2014). In India, its flour is mainly used to make bread, chapattis, cookies, and snacks. However, in many countries it is still grown generally for fodder, birdseed, silage, and hay.

Recently, the health-benefiting properties of millets have gained importance in nutritional and medicinal research. Foxtail millet is widely used not only as an energy source for pregnant and lactating women, but also for sick people and children, and especially for people with diabetes. It is reported to reduce the blood sugar concentration in women diabetics (Sema and Sarita 2002; Dwivedi et al. 2012). Foxtail millet consumption is very important for type-II diabetes patients as it helps in reducing blood glucose concentration, glycosylated haemoglobin, and serum lipids (Thathola et al. 2010). In China it is used to cure rheumatism. The germinated seed of yellow-seeded cultivars is astringent, digestive, emollient, and stomachic. It is used in the treatment of dyspepsia, poor digestion, and food stagnancy in the abdomen (www.agrisources.com/herbs/setariaitalica). Thus, foxtail millet is a versatile crop.

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