



ISSN: 2230-9926

Available online at <http://www.journalijdr.com>

IJDR

International Journal of Development Research

Vol. 13, Issue, 09, pp. 63660-63682, September, 2023

<https://doi.org/10.37118/ijdr.27135.09.2023>



REVIEW ARTICLE

OPEN ACCESS

ORIGIN, DOMESTICATION, TAXONOMY, BOTANICAL DESCRIPTION, GENETICS AND CYTOGENETICS, GENETIC DIVERSITY, BREEDING OF FOXTAIL MILLET (*Setaria italica* (L.) Beauv.)

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ARTICLE INFO

Article History:

Received 10th June, 2023

Received in revised form

27th July, 2023

Accepted 28th August, 2023

Published online 29th September, 2023

KeyWords:

Foxtail millet, Origin, Domestication, Taxonomy, Botanical Description, Breeding.

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ABSTRACT

Foxtail millet belongs to the Family Poaceae, Subfamily Panicoideae, Genus *Setaria* and Species *Setaria italica* (L.) P. Beauvois. Foxtail millet scientific name *Setaria italica* (also known as *Panicum italicum* L.), is an annual herb cultivated for human consumption. Among millet he is the second most widely cultivated and is the most cultivated millet species in Asia. Foxtail millet is an annual grass grown for human food. It is the second-most widely planted species of millet, and the most grown millet species in Asia. The oldest evidence of foxtail millet cultivation was found along the ancient course of the Yellow River in Cishan, China, carbon dated to be from around 8,000 years before present. Foxtail millet has also been grown in India since antiquity. There are three to four foxtail varieties available in the market, namely Moharia, Maxima, Nana and Indica. Foxtail millets have a sweet and nutty flavour and are eaten as instant foods, ready-to-eat products, rice flour, etc. Apart from the culinary uses, it is a farmer-friendly and health-friendly crop; making it "good for you" (due to its nutritional value), and "good for the world" (as it requires less water and other factors for cultivation). In India, foxtail millet is an important crop in its arid and semi-arid regions. In South India, it has been a staple diet among people for a long time from the Sangam period. It is referred to often in old Tamil texts and is commonly associated with Lord Muruga and his consort Valli. Foxtail millet, also known as Italian millet or German millet, belongs to Poaceae family and is cultivated globally, including in India. It is also a staple food and feed in several regions of Asia and Africa. Foxtail millet is also known as dwarf setaria, foxtail bristle-grass, giant setaria, green foxtail, Italian millet, German millet, and Hungarian millet. Names for foxtail millet in Indian languages include: Assamese: *koni dhaan*), Bengali: *kaon dana*, Hindi: *Kangni*, Gujarati: *kang*, Kannada: *navane, navanakki*, Malayalam: *thina*, Marathi: *kang* or *rala*, Odia: *kaṅgu, ṭāṅgaṇa*, Punjabi: *Kangni*, Sanskrit: *priyangu, kangu*, Tamil: *thinai, iradi, enal, kangu, kavalai, or kambankorai; nuvanam* (millet flour) and Telugu: *korralu* or *korra*. It is rich in dietary fibre, protein, vitamins and minerals, and low in fat. Studies show that people who consume foxtail millet in their diet have a lower probability of suffering from diabetes as it doesn't increase the blood sugar levels immediately but slowly releases glucose into the bloodstream. It is rich in dietary fibre and minerals like iron and copper. Due to this, it helps to reduce the levels of bad cholesterol and keeps the immune system strong as well. It is gluten free and improves digestion. It is high in antioxidants, prevents Cancer, has high calcium content and maintains bone health. It helps in weight loss, and it has anti-aging properties as well. The cultivation of foxtail millets began in 8700 BC in China. In India, these are widely grown in Karnataka, Andhra Pradesh, Maharashtra and Tamil Nadu (Singh, 2023). In this review article on Origin, Domestication, Taxonomy, Botanical Description, Genetics and Cytogenetics, Genetic Diversity, Breeding, Uses, Nutritional Value and Health Benefits of Foxtail Millet are discussed.

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Citation: K.R.M. Swamy. 2023. "Origin, domestication, taxonomy, botanical description, genetics and cytogenetics, genetic diversity, breeding of foxtail millet (*Setaria italica* (L.) Beauv.)". International Journal of Development Research, 13, (09), 63660-63682.

INTRODUCTION

Foxtail millet belongs to the Family Poaceae, Subfamily Panicoideae, Genus *Setaria* and Species *Setaria italica* (L.) P. Beauvois (Wikipedia, 2023). Millet, scientific name *Setaria italica* (also known as *Panicum italicum* L.), is an annual herb cultivated for human consumption. Among millet he is the second most widely cultivated and is the most cultivated millet species in Asia (Academic, 2023). The earliest evidence of millet cultivation was found along the

ancient course of the Yellow River in Qishan, China, and was carbon dated to about 8,000 years ago (Academic, 2023). Millet was cultivated in India since ancient times. Other names for this species include dwarf setaria, millet, giant setaria, green foxtail, Italian millet, German millet, and Hungarian millet (Academic, 2023). The cultivation of foxtail millets began in 8700 BC in China. In India, these are widely grown in Karnataka, Andhra Pradesh, Maharashtra and Tamil Nadu (Singh, 2023). Foxtail millet is one of the world's oldest cultivated crops. Foxtail was the most important plant food in

the neolithic culture in China, and its domestication and cultivation was the earliest identifiable manifestation of this culture (Baltensperger and Cai, 2004). There are three to four foxtail varieties available in the market, namely Moharia, Maxima, Nana and Indica (Singh, 2023). Foxtail millets have a sweet and nutty flavour and are eaten as instant foods, ready-to-eat products, rice flour, etc. Apart from the culinary uses, it is a farmer-friendly and health-friendly crop; making it “good for you” (due to its nutritional value), and “good for the world” (as it requires less water and other factors for cultivation) (Singh, 2023). Foxtail millets are a host of nutrients; let us learn more about the health benefits of adding foxtail millets to your dietary routine (Singh, 2023). Millets are considered nutri-cereals which play a crucial part in overcoming malnutrition and have a significant role in improving the status of human health. Foxtail millet also known as Italian millet or German millet, belongs to Poaceae family and is cultivated globally, including in India. It is also a staple food and feed in several regions of Asia and Africa (Moharil *et al.*, 2019). Foxtail is recognized as a diploid ($2n = 2x = 18$), but is closely related to many tetraploid and higher ploidy level species (Baltensperger and Cai, 2004).

Foxtail millet is also known as dwarf setaria, foxtail bristle-grass, giant setaria, green foxtail, Italian millet, German millet, and Hungarian millet (Wikipedia, 2023); Hungarian Millet or Hungarian Grass, Japanese Millet, Siberian Millet, Golden Wonder, Holy Terror, Gold Mine (Chestofbooks, 2023); Chinese Millet, Foxtail Bristle Grass, Dwarf Setaria, Hay Millet, German Millet, Giant Setaria Hungarian Millet, Japanese Millet, Italian Millet, Red Rala, Liberty Millet and Hungarian millet (SM, 2017); dwarf setaria, foxtail bristle grass, German millet, giant setaria, green bristle grass, green foxtail, green foxtail millet, Hungarian millet, Italian millet, wild foxtail millet, nunbank setaria (Heuzé *et al.*, 2020); Italian millet, German millet (En). Panis, millet des oiseaux, millet d'Italie (Fr). Painço, milho painço, milho painço de Itália (Po). Kimanga (Sw) (Brink, 2006). Names for foxtail millet in Indian languages include: Assamese: *koni dhaan*), Bengali: *kaon dana*, Hindi: *Kangni*, Gujarati: *kang*, Kannada: *navane*, *navanakki*, Malayalam: *thina*, Marathi: *kang* or *rala*, Odia: *kaṅgu, tāṅgaṇa*, Punjabi: *Kangni*, Sanskrit: *priyangu, kangu*, Tamil: *thinai*, *iradi*, *enal*, *kangu*, *kavalai*, or *kambankorai*; *nuvanam* (millet flour) and Telugu: *korralu* or *korra* (Wikipedia, 2023; Rutuja, 2023; Academic, 2023; PFAF, 2023). It is also known by different names in different parts of India as – Kangni or Kakum in Hindi, Navane in Kannada, Tenai in Tamil, Korra in Telugu, Rala or Kang in Marathi, Kanghu or Kangam in Odiya, Kang in Gujarati and Thina in Malayalam (Hariprasanna, 2020).

It is rich in dietary fibre, protein, vitamins and minerals, and low in fat. Studies show that people who consume foxtail millet in their diet have a lower probability of suffering from diabetes as it doesn't increase the blood sugar levels immediately but slowly releases glucose into the bloodstream. It is rich in dietary fibre and minerals like iron and copper. Due to this, it helps to reduce the levels of bad cholesterol and keeps the immune system strong as well. It is gluten free and improves digestion. It is high in antioxidants, prevents Cancer, has high calcium content and maintains bone health. It helps in weight loss, and it has anti-aging properties as well (Origin, 2020). In China, foxtail millet was the main staple food in the north before Sung Dynasty, when wheat started to become the main staple food. It is still the most common millet and one of the main food crops in the dry northern part of the country, especially among the poor. In Southeast Asia, foxtail millet is commonly cultivated in its dry, upland regions. In Europe and North America it is planted at a moderate scale for hay and silage, and to a more limited extent for birdseed (Wikipedia, 2023). Foxtail millet is an annual grass grown for human food. It is almost unknown in Maharashtra and elsewhere. It has the longest history of cultivation among the millets, having been grown in India since antiquity. Among the millets, foxtail millet is an important food for many people in the semi-arid regions where the rainfall is inadequate. Foxtail millet is said to have its origin in Eastern Asia. This crop has sustained the lives of the poorest rural people and will continue to do so in the foreseeable future. Therefore, and because this crop is mostly consumed by disadvantaged groups,

they are often referred to as ‘coarse grain’ or ‘poor people’s crop’ (Rutuja, 2023).

Foxtail Millet is an important food plant in many parts of Asia, especially in northern China, where the seed is ground and used for porridge. In America it is not used for human food. The best time to cut for hay is when the majority of the plants are in bloom, as the nutritive value of the stems and leaves is then greatest. When the plants begin to blossom, the bristles of the spikes are still soft and harmless, but when the flowering period is over they become stiff and harsh, produce more or less irritation in the digestive tract of the animals, and are said to sometimes form compact balls in the stomach, causing serious trouble or even death. When used for pasture, millet should be grazed before the heads are formed. When grown for hay or pasture, thirty pounds of seed should be sown to the acre; when grown for seed production, twenty pounds are sufficient (Chestofbooks, 2023). It is one of the ten small millets and is cultivated in 23 countries. Foxtail millet was the most important plant food in the Neolithic culture in China, and its domestication and cultivation was the earliest identifiable manifestation of this culture, the beginning of which has been estimated over 4,000 years ago (ICRISAT, 2023).

The foxtail millet is valued as a crop of short duration, which is good as food, feed and fodder. In general, grain yield levels of foxtail millet are low in comparison with other staple cereals. The greater use of diverse germplasm in breeding is suggested as a means to improve the productivity of this crop (ICRISAT, 2023). The important foxtail millet growing districts in Andhra Pradesh are Anantapur, Kurnool, Prakasam and Guntur, while Mahaboob Nagar and Rangareddy districts are important in Telangana. In Karnataka it is mostly grown in Bellary, Koppal, Chitradurga, Belgaum, Gadag, Davangere and Dharwad (Hariprasanna, 2020). It can grow over a wide range of altitudes ranging from sea level to 2000 m above mean sea level. Foxtail millet is fairly tolerant to drought; it can escape some droughts because of early maturity. Due to its short life cycle, it can be grown as a short-term catch crop (Gupta *et al.*, 2012). It is also cultivated as a dry land crop under marginal and sub-marginal lands. It requires water in the later stages of the crop growth but cannot tolerate water logging (Gupta *et al.*, 2012). It is generally assumed that Foxtail Millets developed in prehistoric time from Green Foxtail or Pigeon Grass (*Setaria viridis* (L.) Beauv.), which in many parts of Canada is a troublesome weed; but there seems to be no conclusive proof of this. At any rate, its cultivation goes very far back. It is one of the five holy plants which, according to a command issued 2700 B.C., were sown each year by the emperor of China at a public ceremony. At present it is grown extensively in Central Asia, northern East India, China and Japan. It is also cultivated in southern and eastern Europe, but is there of only secondary importance (Plant guide, 2023).

Countries where the plant has been cultivated are: Afghanistan, Africa, Andamans, Armenia, Asia, Australia, Austria, Azerbaijan, Azores, Bangladesh, Belgium, Britain, Burma, Cambodia, Canada, Central Asia, China, Cyprus, East Africa, East Timor, Egypt, Europe, France, Georgia, Germany, Greece, Guiana, Guyana, Hungary, India, Indonesia, Iran, Iraq, Israel, Italy, Jamaica, Japan, Kenya, Korea, Kyrgyzstan, Laos, Malawi, Malaysia, Manchuria, Mauritius, Mozambique, Myanmar, Nepal, North Africa, North America, Northeastern India, Pacific, Pakistan, Papua New Guinea, Philippines, PNG, Russia, Saudi Arabia, SE Asia, South Africa, Southern Africa, Spain, Sri Lanka, Switzerland, Syria, Taiwan, Tajikistan, Tanzania, Tasmania, Thailand, Timor-Leste, Trinidad & Tobago, Turkmenistan, Ukraine, USA, Vietnam, Yemen, Zimbabwe (PFAF, 2023). The US patent office introduced foxtail millet as a forage crop in 1849. It has since become well adapted to the western Great Plains. Nearly all foxtail millet cultivars grown in the US are the result of selections from land races rather than designed crosses and selections (Baltensperger and Cai, 2004). In this review article on Origin, Domestication, Taxonomy, Botanical Description, Genetics and Cytogenetics, Genetic Diversity, Breeding, Uses, Nutritional Value and Health Benefits of Foxtail Millet are discussed.

ORIGIN AND DOMESTICATION

The antiquity of foxtail millet as a cultivated cereal is uncertain. It probably evolved from spontaneous green foxtail (*S. italica* ssp. *viridis*) under a regime of harvesting and sowing. The species could have been domesticated anywhere across its natural range extending from Europe to Japan. It has been grown in China for about 5,000 yrs. It was an important cereal in the highlands during Yang-shao times. Jars filled with husks of *S. italica* were found at an early farming site at Banpo in Shanxi. The abundance of this cereal in storage and the farming implements associated with Yang-shao cultures strongly suggest that the cereal was cultivated rather than harvested in the wild. The name of the legendary ancestor of the Chow tribe of the loess highlands, Hou Chi, translates literally to mean "Lord of Millets". It is possible that the name refers to *Panicum miliaceum* L. (broomcorn millet), another early cultivated millet of China. Foxtail and broomcorn millets were probably domesticated in China at about the same time. Wang Xiangjin of the Ming dynasty, however, recorded that northerners relied on foxtail millet for their daily food (Rao *et al.*, 1987). Foxtail and broomcorn millets also occur in early agricultural sites from Switzerland and Austria dating back some 3,000 yrs.. The progenitor of broomcorn millet is native to Manchuria, and this species was probably introduced to Europe as a domesticated cereal. Green foxtail millet, native to southern Europe and temperate Asia, could have been independently domesticated in Europe and China. European neolithic site at Baldegy, in which foxtail millet grains occur, to around 3600 B.P. has been reported. The species, however, became widely cultivated in Europe only during the Bronze Age, when the more cold tolerant broomcorn millet spread rapidly across northern Europe. These millets are absent from known neolithic settlements in the Far East from ancient Egypt and from neolithic India (Rao *et al.*, 1987). Foxtail millet is an old crop, grown since 5000 BC in China and 3000 BC in Europe. It probably evolved from the wild *Setaria viridis* (L.) P.Beauv. (green foxtail millet), and it was most probably first domesticated in the highlands of central China, from where it spread to India and Europe soon thereafter. Evidence for this origin, however, is not conclusive and its domestication may have taken place anywhere in the area extending from Europe to Japan, perhaps even several times independently.

several groups, the issue is still ambiguous. It is essential to resolve this issue by studying a large number of accessions with sufficient markers covering the entire genome. Genetic structures were analyzed by transposon display (TD) using 425 accessions of foxtail millet and 12 of the wild ancestor green foxtail (*Setaria italica* subsp. *viridis* (L.) P. Beauv.). We used three recently active transposons (TSI-1, TSI-7, and TSI-10) as genome-wide markers and succeeded in demonstrating geographical structures of the foxtail millet. A neighbor-joining dendrogram based on TD grouped the foxtail millet accessions into eight major clusters, each of which consisted of accessions collected from adjacent geographical areas. Eleven out of 12 green foxtail accessions were grouped separately from the clusters of foxtail millet. These results indicated strong regional differentiations and a long history of cultivation in each region. Furthermore, we discuss the relationship between foxtail millet and green foxtail and suggest a monophyletic origin of foxtail millet domestication (Ryoko Hirano *et al.*, 2011). Several hypotheses regarding the origin and domestication have been proposed and a multiple domestication hypothesis has been widely accepted. A multiple domestication hypothesis with three centers, that is, China, Europe, and Afghanistan–Lebanon has been suggested (Vetriventhan *et al.*, 2016). Foxtail millet [*Setaria italica* (L.) P. Beauv.] is one of the oldest cereals in Eurasia, grown since 5000 BC in China and 3000 BC in Europe. It probably evolved from the wild green foxtail millet—*Setaria viridis* (L.) P. Beauv. The geographical origin of foxtail millet is still a controversial issue. Its domestication could have taken place anywhere across its natural range extending from Europe to Japan, perhaps even several times independently; it was most probably first domesticated in the highlands of central China, from where it spread to India and Europe soon thereafter.. At present, foxtail millet is cultivated all over the world, being most important in China, India, Indonesia, the Korean peninsula and south-eastern Europe. In most countries in the world, foxtail millet is cultivated mainly for production of grains for human consumption. The tiny grains are milled into flour used for preparation of different dishes (puree, cakes). In China, Korea, and Japan, foxtail millet is important for beer preparation, with the sprouted seeds used instead of malt. Thanks to fermentation, various alcoholic beverages are prepared. In Europe, seeds of foxtail millet are used for poultry feeding and plants

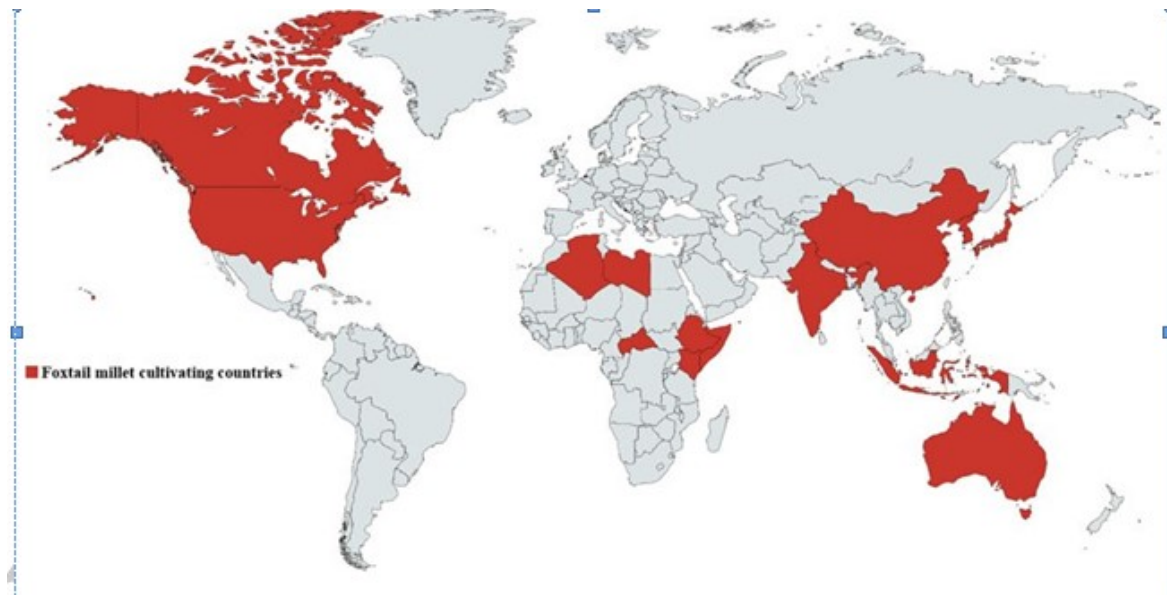


Fig. 1. Geographical distribution of Foxtail millet cultivation (Red color)

Foxtail millet was the ‘panicum’ of the Romans. At present foxtail millet is cultivated all over the world. In tropical Africa it is cultivated to a limited extent in upland areas in East Africa and occasionally recorded elsewhere, e.g. in Cameroon and southern Africa (Malawi, Zimbabwe, Mozambique). In these areas it also occurs as an escape. Foxtail millet is also grown in South Africa and Lesotho (Brink, 2006). Although the origin and domestication process of foxtail millet (*Setaria italica* subsp. *italica* (L.) P. Beauv.) has been studied by

are cultivated as a fodder crop for green biomass or hay production (Hermuth *et al.*, 2016). Foxtail millet was first naturalized in China. The evidence shows the domestication of Foxtail millet in the Middle East and Europe which dates about 4000 years BP. The phylogenetic analyses show the green millet and foxtail millet is associated and the Foxtail millet is naturalized derivative of the green millet. Currently, Foxtail millet is sophisticated in Europe, America, Asia, Africa and Australia. The evidence (early) shows that it was cultivated in China

by Peiligang culture. Though the common millet was also cultivated, Foxtail millet becomes prevalent in the Yangshao culture. About 6000 BC, it was cultivated in the Iron Age at Near East (SM, 2017). 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). Green foxtail (*S. viridis*) is the wild ancestral form of modern cultivated foxtail millet (*S. italica*). It has been proposed that the prime center of evolution and diversification of foxtail millet was East Asia, specifically China and Japan (Fig. 1). 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. 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. 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. In India, it is cultivated primarily in Karnataka, Andhra Pradesh, Rajasthan, Madhya Pradesh and Chhattisgarh, and Tamil Nadu (Fig. 2) (Singh *et al.*, 2017).

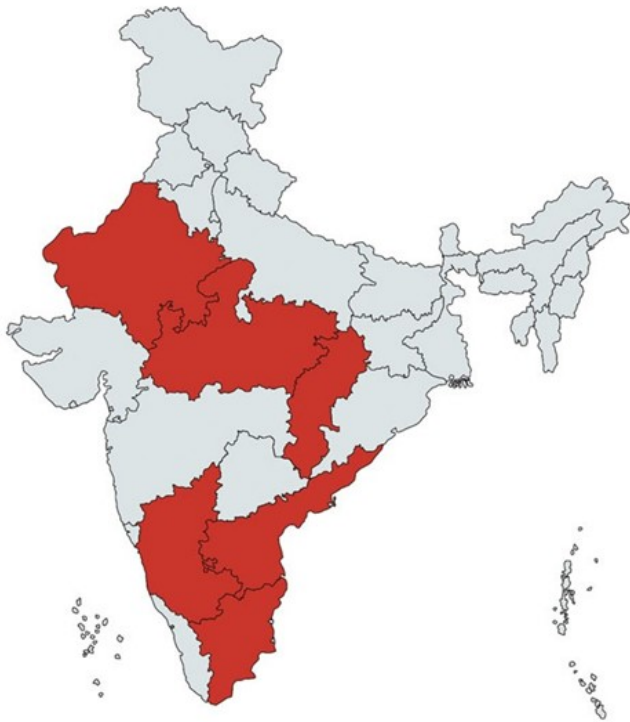


Fig. 2. Geographical distribution of Foxtail millet cultivation in India (Red color)

Foxtail millet or navane was first domesticated in China and then became a cereal cultivated throughout Eurasia. In India, foxtail millet is still an important crop in arid and semi-arid regions. In South India, it has been a staple diet among people for a long time (Origin, 2020). Foxtail millet is believed to be originated in China. Foxtail millet was the most important plant food in the neolithic culture in China. In Russia, foxtail millet has been cultivated since ancient times and there is evidence that it was grown as long as 1,500 years ago. According to Vavilov (1926), the principal center of diversity for foxtail millet is East Asia, including China and Japan. From China or Central Asia it spread to India and European countries. However, a multiple domestication hypothesis has been widely accepted because of its cultivation about 4000 years ago at Europe. It is adapted to a wide range of elevations, soils and temperatures. In India, at present, foxtail millet is cultivated on a limited area in Karnataka, Telangana, Andhra Pradesh, Maharashtra, Tamil Nadu, Rajasthan, Madhya Pradesh, Uttar Pradesh and north eastern states

(Hariprasanna, 2020). Foxtail millet may have originated from China, where its cultivation dates back to 5000 BC. It probably spread from the highlands of Central China towards India and Europe and can now be found all over the world. The major production centres are China and India. In Africa, foxtail millet can be found in upland areas in East Africa, Cameroon and Southern Africa. In Europe, where it used to be cultivated as a summer crop until the 17th century, it has become marginal and Central Europe is now the main area of production. Foxtail millet is a fast-growing summer annual and crop duration varies from 60 to 120 days. It is very adaptive and can be cultivated from sea level up to an altitude of 2000 m. It grows best in places where annual rainfall ranges from 500 to 700 mm of summer rain. However, it continues growing with under 300-400 mm annual rainfall and in semi-arid areas with less than 125 mm rainfall during the 3 to 4 months of growth. Foxtail millet is frost sensitive and grows better between 16 and 26°C, though it has much larger temperature tolerance (5-35°C). It thrives on many kinds of soils, from sandy to heavy clay soils, but not on saline soils. The pH should be in the 5.5-8.3 range and soils should not be water-logged (Heuzé *et al.*, 2020).

Foxtail millet was considered to be domesticated in the highlands of central China. The main production regions of the world include China, parts of India, Afghanistan, Central Asia, Manchuria, Korea, and Georgia. It is also one of the specialty crops in Japan. In Asia, it is mainly grown for human consumption. It was recently introduced in the United States for hay and silage. Because of its short growth cycle, it is a suitable crop for nomads, and was probably brought to Europe during the Stone Age. It is necessary to understand that the wild ancestor of foxtail millet has been securely identified as *Setaria viridis*, which is inter-fertile with foxtail millet; wild or weedy forms of foxtail millet also exist. The primary difference between the wild and cultivated forms is their seed dispersal biology. Wild and weedy forms shatter the seeds while cultivars retain them. The most primitive confirmation of the cultivation of this grain comes from the Peiligang culture of China, which also cultivated proso millet. Out of the all suggestions lately, the Cishan culture of China has been recognized as the most basic to domesticate foxtail millet around 6500–5500 BC. The most primitive evidence for foxtail millet farming outside of its native distribution is at Chengtoushan in the Middle Yangtze River region, dating back to around 4000 BC. *S. viridis* is the antecedent of *S. italica* as confirmed by genetic comparison. During its journey in southern China, foxtail millet reached the Chengdu Plain around 2700 BC and Gantuoyan, near the Vietnamese border in around 3000 BC. Foxtail millet also reached Taiwan in around 2800 BC and the Tibetan Plateau (Karuo) in around 3000 BC. *Setaria italica* likely reached Southeast Asia via multiple routes. In the beginning the evidences for foxtail millet rises in south east Asia from different sites of central Thailand including Khao Wong Prachan Valley, along with the site at Non Pa Wai suggesting the primitive date around 2300 BC. The most primitive evidence of origin of foxtail millet in East Siberia found from the archaeological site at Krounovka in Primorsky Krai, dating to around 3620–3370 BC. The earliest direct claim for foxtail millet in Korea come from Dongsam-dong Shell Midden, a Jeulmun site in southern Korea around 3360 BC (Joshi *et al.*, 2021).

Foxtail millet, is an annual grass grown for human food. It is the second-most widely planted species of millet, and the most grown millet species in Asia. The oldest evidence of foxtail millet cultivation was found along the ancient course of the Yellow River in Cishan, China, carbon dated to be from around 8,000 years before present. Foxtail millet has also been grown in India since antiquity (Wikipedia, 2023). It is generally assumed that Foxtail Millets developed in prehistoric time from Green Foxtail or Pigeon Grass (*Setaria viridis* (L.) Beauv.), which in many parts of Canada is a troublesome weed; but there seems to be no conclusive proof of this. At any rate, its cultivation goes very far back. It is one of the five holy plants which, according to a command issued 2700 B.C., were sown each year by the emperor of China at a public ceremony. At present it is grown extensively in Central Asia, northern East India, China and

Japan. It is also cultivated in southern and eastern Europe, but is there of only secondary importance (Chestofbooks, 2023).

Foxtail millet is an old crop, grown since 5000 B.C. in India. In fact it is so old that no wild plant of the species is known to exist today. It probably evolved from the wild *Setaria viridis* (green *Setaria italica*). Its domestication may have taken place anywhere in the area extending from Europe to Japan, perhaps several times independently. *Setaria italica* (L.) was the 'panicum' of the Romans. In India, Foxtail millet has been mentioned in some of the oldest Yajurveda texts, identifying foxtail millet as priyangava, thus indicating that its consumption was very common, pre-dating to the Indian Bronze Age (4,500BC). In fact, these seeds are believed to have been around since Stone Age. It has naturally adapted to the climate of India just as our own bodies have. It is also mentioned in rudrasuktam highlighting its presence and consumption during those times. It was known to be one of the devdhanya which includes satu, sava, etc. Not only has Yajurveda mentioned Rala, Rigveda and Atharvaveda have also suggested the uses of Rala. Ayurveda, an Indian scripture, includes it in a trunadhanya, kudhanya category. Ayurveda suggests many uses of rala as it is a major source of nutrients. Charak (physician) and Sushruta (surgeon) have mentioned Foxtail millet in their writings. The great physician, Vaagbhata has written in his texts that rala aids in the recovery of fractures. Also, in Kalidasa's epic play Abhijnana Shakuntalam written in 1st century, sage Kanva pours rala in Shakuntala's hands while bidding a tearful farewell at Dushyanta's court (Rutuja, 2023). The wild predecessor of millet has been definitively identified as *Setaria viridis*, and is hybridizable with millet. Wild or weedy forms of millet also exist. Zohari and Hopp point out that the main difference between wild and cultivated forms "is in the biology of seed dispersal: wild and weedy forms crush seeds, while cultivated forms retain seeds." The reference genome of millet was completed in 2012. Genetic comparisons also confirm that *S. viridis* is the predecessor of *S. italica*. The earliest evidence of cultivation of this grain comes from the Peiligang culture of China, which also cultivated *Panicum miliaceum*. However, it was not until the Yangshao culture that millet became a major crop. More recently, the Qishan culture of China has been identified as the earliest domesticated millet, around 6500-5500 BC. The earliest evidence of foxtail millet cultivation outside its natural range is found on Chengtuo Mountain in the middle reaches of the Yangtze River, and is dated to around 4000 years. B.C. In southern China, millet reached the Chengdu Plain (Baotun) around 2700 BC and the Guangxi Zhuang Autonomous Region (Gantuyan near the Vietnamese border) around 3000 BC. Millet also reached Taiwan (Nanguanli, Dapenkeng culture) around 2800 BC and the Tibetan plateau (Kalu) around 3000 BC. Millet is thought to have reached Southeast Asia via multiple routes. The earliest evidence of foxtail millet in Southeast Asia comes from various sites in the Khao Wong Prachan valley of central Thailand, with the site at Nong Pa Wai directly dating AMS to about 2300 BC, indicates the earliest date. Eastern Siberia originates from the site of Krnovka 1 in Primorsky Krai, dating from about 3620 to 3370 BC. The earliest direct evidence of foxtail millet in Korea comes from the Dongsam-dong shell mound, a Jemun site in southern Korea, with a direct AMS date of around 3,360 BC.

In Japan, the earliest evidence of foxtail millet comes from a Jomon site in Usujiri, Hokkaido, dating back about 4,000 years. Millet later spread to Europe. Charred seeds first appeared in Central Europe in the 2nd millennium BC. The earliest clear evidence of cultivation in the Near East is at Tyrehöyük, Turkey, at the Iron Age level, with an uncorrected radiocarbon date of about 600 BC (Academic, 2023). The wild ancestor of foxtail millet has been securely identified as *Setaria viridis*, which is interfertile with foxtail millet; wild or weedy forms of foxtail millet also exist. Zohary and Hopf note that the primary difference between the wild and cultivated forms is "their seed dispersal biology. Wild and weedy forms shatter their seed while the cultivars retain them." The reference genome for foxtail millet was completed in 2012. Genetic comparisons also confirm that *S. viridis* is the antecedent of *S. italica*. The earliest evidence of the cultivation of this grain comes from the Peiligang culture of China, which also cultivated *Panicum miliaceum*, but foxtail millet became the

predominant grain only with the Yangshao culture. More recently, the Cishan culture of China has been identified as the earliest to domesticate foxtail millet around 6500–5500 BC. The earliest evidence for foxtail millet cultivation outside of its native distribution is at Chengtoushan in the Middle Yangtze River region, dating to around 4000 BC. In southern China, foxtail millet reached the Chengdu Plain (Baodun) at around 2700 BC and Guangxi (Gantuoyan [de], near the Vietnamese border) at around 3000 BC. Foxtail millet also reached Taiwan (Nankuanli, Dapenkeng culture) at around 2800 BC and the Tibetan Plateau (Karu) at around 3000 BC. Foxtail millet likely reached Southeast Asia via multiple routes. The earliest evidence for foxtail millet in Southeast Asia comes from various sites in the Khao Wong Prachan Valley in central Thailand, with the site at Non Pa Wai [de] providing the earliest date with direct AMS dating to around 2300 BC. The earliest evidence for foxtail millet in East Siberia comes from the archaeological site at Krounovka 1 in Primorsky Krai, dating to around 3620–3370 BC. The earliest direct evidence for foxtail millet in Korea come from Dongsam-dong Shell Midden, a Jeulmun site in southern Korea, with a direct AMS date of around 3,360 BC. In Japan, the earliest evidence for foxtail millet comes from the Jōmon site at Usujiri in Hokkaido, dating to around 4,000 BP. Foxtail millet arrived in Europe later; carbonized seeds first appear in the second millennium BC in central Europe. The earliest definite evidence for its cultivation in the Near East is at the Iron Age levels at Tille Hoyuk in Turkey, with an uncorrected radiocarbon date of about 600 BC (Wikipedia, 2023).

TAXONOMY

Foxtail millet belongs to the Family Poaceae, Subfamily Panicoideae, Genus *Setaria* and Species *Setaria italica* (L.) P. Beauvois (Singh *et al.*, 2017; Wikipedia, 2023; Rutuja, 2023). Millet, scientific name *Setaria italica* (also known as *Panicum italicum* L.), is an annual herb cultivated for human consumption. Among millet he is the second most widely cultivated and is the most cultivated millet species in Asia (Academic, 2023). *Setaria* comprises about 100 species distributed in the tropics, subtropics and temperate regions. Foxtail millet is the most economically valuable species of the genus. Several wild *Setaria* species are harvested for their seeds, *e.g.* *Setaria finita* Launert in Namibia. *Setaria sphacelata* (Schumach.) Stapf & C.E.Hubb. ex M.B.Moss is cultivated as a forage throughout the tropics and its grains are gathered as a famine food in Africa. The grains of *Setaria pumila* (Poir.) Roem. & Schult. are also eaten as a famine food, *e.g.* in Mali, Burkina Faso, Sudan and Ethiopia, but it is more important as a forage. *Setaria verticillata* (L.) P.Beauv. is a forage plant, but also collected as a famine food, *e.g.* in Niger, Sudan and Namibia. *Setaria italica* is a 'crop-weed complex', *i.e.* with wild and cultivated types. These types show no crossing barriers and isozyme analysis and molecular studies have confirmed their similarity. The wild types are considered to represent *Setaria viridis* (green foxtail millet), the cultivated ones *Setaria italica* (foxtail millet). Green foxtail millet occurs worldwide as a variable, annual weed, especially common in temperate regions. It differs from foxtail millet in its completely caducous spikelets, upper glume about as long as the spikelet and more roughly papillose lemma. It is sometimes considered a subspecies of *Setaria italica*: subsp. *viridis* (L.) Thell. It is also known as green bristle grass, and is one of the world's most noxious weeds, but it is sometimes used as fodder or for medicinal purposes. Foxtail millet is very variable and numerous cultivars exist, differing in time to maturity, plant height, size, habit and structure of inflorescence, number, colour and length of bristles, and colour of grain. Primitive cultivars have numerous, strongly branched stems (like green foxtail millet), while advanced cultivars produce a single stem with a large, solitary inflorescence (Brink, 2006).

Cultivated foxtail millets were recognized by Linnaeus (1753) as *Panicum italicum*. Variants within the species were later recognized as *Panicum germanicum* Mill. and *P. glomeratum* Moench. These taxa were transferred to *Setaria* and combined into *S. italica* (foxtail millets) and transferred the weedy *P. viride* L. (green foxtail) to *Setaria*. Foxtail millet and the weedy green foxtail are morphologically and genetically allied. Some cultivars of *S. italica* in

southeastern Europe and in Afghanistan resemble green foxtail except for their lack of efficient natural seed dispersal. Foxtail millet also crosses naturally and experimentally with green foxtail to produce fertile hybrids. For these reasons green foxtail and foxtail millet are taxonomically considered to be conspecific; and the cultivated taxa are recognized as *S. italica* ssp. *italica* and the spontaneous taxa as *S. italica* ssp. *viridis*. *Setaria italica* ssp. *viridis* is based on *S. viridis*. Spontaneous green foxtail is extensively variable, widely distributed in temperate Eurasia, and extensively naturalized as a weed in the temperate parts of the New World. It is primarily an urban weed, but a robust race is an obnoxious weed of agricultural land in the American Corn Belt. Green foxtail is typically a small, erect or decumbent plant up to 1.5 m tall, with several culms that are strongly branched. Leaf blades are linear-lanceolate, essentially glabrous, and up to 29 cm long, but usually shorter. Panicles are spike-like and densely flowered, usually less than 10 cm long, with 0.5-1.5 cm long branches bearing clusters of several spikelets, each subtended by one to three bristles that exceed the 2.0-2.5 mm long spikelets in length. Spikelets are elliptic, with the lower glume about one third the length of the spikelet, and the upper glume about as long as the lemma. Spikelets disarticulate from the rachis below the glumes. The single grain is tightly enclosed by the indurate lemma and palea. Giant green foxtail, a weed foxtail of corn fields in the American Midwest, also occurs across the species range in Eurasia. It is more robust (1.0-2.5 m tall) than common green foxtail and has larger panicles (up to 20 cm long), elongated panicle branches (up to 4 cm long), and an erect growth habit. It was suggested that giant green foxtail originated from cultivated foxtail millets through mutations that introduced natural seed dispersal. They more likely represent derivatives of hybrids between wild and cultivated *S. italica*. Foxtail millet is highly autogamous, but natural hybrids between wild and cultivated taxa do occur. Hybrids produced were about 50% sterile although meiotic chromosome behavior was regular. Similar hybrids produced were fully fertile, and derivatives of these crosses resembled spontaneous giant green foxtail in morphological detail. Genetic studies indicate that spikelet disarticulation is controlled by two complementary dominant genes, and hybrids as well as some of their derivatives were characterized by wild-type seed dispersal. *Setaria italica* ssp. *italica* is based on *S. italica*. Including all cultivated foxtail millets, it differs consistently from ssp. *viridis* only in having lost the ability of natural seed dispersal. It depends on man for sowing in suitable habitats. Foxtail millet is morphologically variable and widely grown as a cereal across temperate, subtropical, and tropical Eurasia (Rao *et al.*, 1987).

The species has undergone extensive morphological changes under domestication. As in other cereals, the primary phenotypic change was a loss of efficient natural seed dispersal. Persistent spikelets at maturity facilitate harvesting. Those cultivars from southeastern Europe and from Afghanistan that resemble wild foxtail millet in vegetative and inflorescence structure differ from it in that their spikelets do not disarticulate at maturity. A second universal characteristic of domesticated cereals is a tendency toward uniform plant maturity. This is achieved through a combination of synchronized tillering and apical dominance. The number of tillers is usually reduced under domestication, as are number of inflorescence-bearing branches on each culm. Apical dominance can lead to a loss of all but one culm and to the production of a single terminal inflorescence. In foxtail millets, primitive cultivars have numerous, strongly branched culms as is characteristic of spontaneous green foxtail, while highly evolved cultivars produce a single culm with a large, solitary inflorescence. Reduction in number of inflorescences per plant is usually associated with an increase in inflorescence size. This is due to an increase in the length of the primary axis and an increase in number of spikelets on each inflorescence branch. It was demonstrated that the number of fertile spikelets per inflorescence is correlated with an increase in number of branches and degree of inflorescence branching. The primary branches elongate to accommodate the increased number of spikelets, and in some cultivars secondary branches become so crowded as to give the inflorescence a lobed appearance (Rao *et al.*, 1987). 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 (Singh *et al.*, 2017).

Racial classification of cultivated foxtail millets

Foxtail millet are commonly divided into two cultivar complexes on the basis of inflorescence structure. Cultivars with large, pendulous inflorescences are included in group *maxima*, and those with smaller, erect inflorescences, in group *moharia* (germanicum). Within groups, cultivars are recognized on the basis of fruit color, bristle length, and length of lateral inflorescence branches. Foxtail millets are classified into ssp. *moharium* to include cultivars with numerous culms and small, cylindrical inflorescences, and ssp. *maxima* to include cultivars with one or a few culms and large inflorescences. They indicated that *maxima* cultivars are grown from Russian Georgia (Transcaucasia) to Japan, while *moharium* cultivars are the principal foxtail millet in Europe (Rao *et al.*, 1987). The study of collections from across the range of *S. italica* cultivation suggests three morphologically distinct complexes. These complexes are recognized as races. They are artifacts of man's agricultural activities and do not deserve formal taxonomic status. Foxtail millet has abundant within-species diversity. Rao *et al.* (1987) suggested three races of foxtail millet based on the comparative morphology of the foxtail millet accessions:

1) Race *moharia*: Cultivars of race *moharia* often resemble members of wild ssp. *viridis* (green foxtail) in phenotype, except that they have lost the ability of natural seed dispersal. Plants are 25-100 cm tall, with 5-52 (av. 8.6) tillers per plant. Tillers are usually branched to produce a well-developed terminal inflorescence and several, smaller lateral inflorescences. Terminal inflorescences are erect or nodding at maturity and 5-20 cm long. Panicle branches are short and compactly arranged on the primary axis. Bristles are well developed or more rarely shorter than the spikelets. At Patancheru (India) these cultivars start to flower 32-50 days after sowing. Race *moharia* is cultivated in southeastern Europe, southwestern Russia, Afghanistan, and Pakistan. Cultivars from Afghanistan have small inflorescences with unusually large grains. Phenotypically similar cultivars occur in Manchuria and northeastern China. Discriminant function analysis suggests close affinities with primitive Manchurian cultivars as well as with the race *indica* (Rao *et al.*, 1987).

2) Race *maxima*: This race, extensively variable, is characterized by spikelets closely arranged on elongated lateral branches, giving the inflorescence a lobed appearance. Plants are 45-100 cm tall, with 1-8 (av. 1.6) unbranched tillers, each bearing a terminal inflorescence. Two inflorescence types are recognized. Plants from eastern China, Japan, and Korea are tall, with large, pendulous inflorescences 12-30 cm long. They commonly have well-developed bristles. Plants with smaller, essentially erect inflorescences occur in northwestern China and Mongolia. These commonly have short bristles and often have the panicle branches tightly packed along the primary axis. Race *maxima* was introduced into the United States, where it is grown as bird feed. It also occurs in Nepal and Assam, along the southern foothills of the Himalaya, and in Russian Georgia (Rao *et al.*, 1987).

3) Race *indica*: Foxtail millet is well adapted to dryland agriculture across tropical and subtropical southern Asia. It is particularly important as a cereal among hill tribes of the western and eastern Ghats of Central India and in Sri Lanka. Foxtail millet is frequently grown as a secondary crop with *Sorghum bicolor* (L.) Moench (grain sorghum). It is extensively variable in India, and race *indica* was probably derived from a combination of *moharia* cultivars from southwestern Asia and *maxima* cultivars from China (Rao *et al.*, 1987).

These races can be further divided into 10 subraces (aristata, fusiformis, and glabra in *moharia*; compacta, spongiosa, and assamense in *maxima*; and erecta, glabra, nana, and profusa in *indica*). Later it was added the race nana along with *maxima*, *moharia*, and *indica* and described the plants that resemble the wild

green millet, and are very short and slender, with many tillers, very short panicles with poor yield performance, and early maturity as a separate race nana (Rao *et al.*, 1987).

Synonyms (Wikipedia, 2023).

- 1) *Alopecurus caudatus* Thunb.
- 2) *Chaetochloa germanica* (Mill.) Smyth
- 3) *Chaetochloa italica* (L.) Scribn.
- 4) *Chamaeraphis italica* (L.) Kuntze
- 5) *Echinochloa erythrosperma* Roem. & Schult.
- 6) *Echinochloa intermedia* Roem. & Schult.
- 7) *Isophorus italicus* (L.) Nash
- 8) *Oplismenus intermedius* (Hornem.) Kunth
- 9) *Panicum aegyptiacum* Roem. & Schult. nom. inval.
- 10) *Panicum asiaticum* Schult. & Schult.f. nom. inval.
- 11) *Panicum chinense* Trin.
- 12) *Panicum compactum* Kit. nom. inval.
- 13) *Panicum elongatum* Salisb. nom. illeg.
- 14) *Panicum erythrospermum* Vahl ex Hornem.
- 15) *Panicum germanicum* Mill.
- 16) *Panicum germanicum* Willd. nom. illeg.
- 17) *Panicum globulare* (J.Presl) Steud.
- 18) *Panicum glomeratum* Moench nom. illeg.
- 19) *Panicum intermedium* Vahl ex Hornem.
- 20) *Panicum italicum* L.
- 21) *Panicum itieri* (Delile) Steud.
- 22) *Panicum macrochaetum* (Jacq.) Link
- 23) *Panicum maritimum* Lam.
- 24) *Panicum melifrugum* Schult. & Schult.f. nom. inval.
- 25) *Panicum miliaceum* Blanco nom. illeg.
- 26) *Panicum moharicum* (Alef.) E.H.L.Krause
- 27) *Panicum panis* (Jess.) Jess.
- 28) *Panicum pumilum* Link nom. illeg.
- 29) *Panicum serotinum* Trin. nom. inval.
- 30) *Panicum setaceum* Trin. nom. inval.
- 31) *Panicum setosum* Trin. nom. inval.
- 32) *Panicum sibiricum* Roem. & Schult. nom. inval.
- 33) *Panicum vulgare* Wallr. nom. illeg.
- 34) *Paspalum germanicum* (Mill.) Baumg.
- 35) *Penicillaria italica* (L.) Oken
- 36) *Pennisetum erythrospermum* (Vahl ex Hornem.) Jacq.
- 37) *Pennisetum germanicum* (Mill.) Baumg.
- 38) *Pennisetum italicum* (L.) R.Br.
- 39) *Pennisetum macrochaetum* J.Jacq.
- 40) *Setaria asiatica* Rchb. nom. inval.
- 41) *Setaria californica* Kellogg
- 42) *Setaria compacta* Schur nom. inval.
- 43) *Setaria erythrosperma* (Vahl ex Hornem.) Spreng.
- 44) *Setaria erythrosperma* Hornem. ex Rchb. nom. inval.
- 45) *Setaria flavida* Hornem. ex Rchb. nom. inval.
- 46) *Setaria germanica* (Mill.) P.Beauv.
- 47) *Setaria globulare* J. Presl
- 48) *Setaria globularis* J.Presl
- 49) *Setaria itieri* Delile
- 50) *Setaria japonica* Pynaert
- 51) *Setaria macrochaeta* (Jacq.) Schult.
- 52) *Setaria maritima* (Lam.) Roem. & Schult.
- 53) *Setaria melinis* Link ex Steud.
- 54) *Setaria moharica* Menabde & Erizin
- 55) *Setaria multiseta* Dumort.
- 56) *Setaria pachystachya* Borbás nom. illeg.
- 57) *Setaria panis* Jess.
- 58) *Setaria persica* Rchb. nom. inval.
- 59) *Setaria violacea* Hornem. ex Rchb. nom. inval.
- 60) *Setariopsis italica* (L.) Samp.

Synonyms (Heuzé *et al.*, 2020).

- 1) *Chaetochloa italica* (L.) Scribn.,
- 2) *Chaetochloa viridis* (L.) Scribn.,
- 3) *Chamaeraphis viridis* (L.) Millsp.,

- 4) *Panicum italicum* L.,
- 5) *Panicum pachystachys* Franch. & Sav.,
- 6) *Panicum viride* L.,
- 7) *Setaria italica* subsp. *maxima* (Alef.) Dekapr. & Kasparian,
- 8) *Setaria italica* var. *moharia* Alef. ex Hegi,
- 9) *Setaria pachystachys* (Franch. & Sav.) Matsum.,
- 10) *Setaria viridis* (L.) P. Beauv.,
- 11) *Setaria viridis* subsp. *pachystachys* (Franch. & Sav.) Masam. & Yanagita

BOTANICAL DESCRIPTION

Foxtail millet in India is typically a robust plant with 1-25 (av. 3.4) culms. Inflorescences are 6-30 cm long, with the elongated lateral branches loosely arranged along the primary axis. Peduncles are erect or nodding, with larger inflorescences becoming curved at maturity because of the weight of their grains. Bristles are usually well developed. Some collections from northern India belong typically with race *maxima* and are introduced from China. Collections from Meghalaya have long, slender inflorescences with small spikelets, and those from Assam commonly have short, compact inflorescences. Plants in which the bristles bear a spikelet at the tip occur across the range of foxtail millet cultivation in India. Two collections from Karnataka have stiffly erect, slender panicles with short lateral branches, somewhat resembling cultivated yellow foxtail, *S. pumila*, in inflorescence and spikelet structure. Foxtail millet has one to three bristles below each spikelet, whereas yellow foxtail millet has four or more bristles supporting each spikelet. One to three bristles occur below the spikelet in the Karnataka cultivar (Rao *et al.*, 1987). Foxtail millet grown in the US is typically less than 1.5 m in height with a stem intermediate in size between proso and pearl millet. Head length is variable like pearl millet, but shorter and more lax. Foxtail is self-pollinated for the most part and, with a compact panicle and small florets, it is extremely difficult to cross. Improved techniques have been developed by Melicio Siles and others, but limited directed genetic improvement has been made due to this constraint (Baltensperger and Cai, 2004).

Erect annual grass up to 150(–175) cm tall, tufted, often variously tinged with purple; root system dense, with thin wiry adventitious roots; stem erect, tillering at base, sometimes branched. Leaves alternate, simple; leaf sheath 10–15(–25) cm long, glabrous or slightly hairy; ligule short, fimbriate; blade linear, 15–30(–50) cm × 0.5–2.5(–4) cm, acuminate at apex, midrib prominent, slightly rough. Inflorescence a spike-like panicle 5–30 cm × 1–2(–5) cm, erect or pendulous, continuous or interrupted at base; rachis ribbed and hairy; lateral branches short, bearing 6–12 spikelets. Spikelets almost sessile, subtended by 1–3 bristles up to 1.5 cm long, elliptical, usually about half as long as the bristles, 2-flowered; lower glume small and 3-veined, upper glume slightly shorter than spikelet, 5-veined; lower floret sterile, upper one bisexual with 5-veined lemma and palea, 2 lodicules, 3 stamens and superior ovary with 2 plumose stigmas. Fruit a caryopsis (grain), broadly ovoid, up to 2 mm long, pale yellow to orange, red, brown or black, tightly enclosed by lemma and palea (Brink, 2006). The inflorescence of foxtail millet has a main stalk with shortened side branches bearing spikes and bristles. The inflorescence is a terminal spike, 8–32 cm long, drooping, dense, cylindrical lobed, borne on a thin and very short pedicel. Each spikelet consists of a pair of glumes that embraces two minute flowers. The lower one is sterile whereas the upper one is fertile or bisexual with three stamens and a long oval smooth ovary with two long styles ends feathery. The anthers are yellow or white, ovary surmounted by two long styles and feathery stigmas. Thelodicules are two in number. The grain is oval in shape, shiny, 2 mm in length, tightly enclosed within the thickened lemma and palea; varying in colour from cream to orange, yellow brown to black (Gupta *et al.*, 2012).

Foxtail millet is an erect annual grass between 0.6 and 1.2 m tall, tufted, often variously tinged with purple. Its root system is dense, with thin wiry adventitious roots from the lowest nodes. The stem is erect, slender, tillering from the lower buds, sometimes branched.

Primitive cultivars have numerous, strongly branched stems, while advanced cultivars produce a single stem with a large, solitary inflorescence. Its leaves are alternate, simple; leaf sheath cylindrical, 10–15 (–26) cm long, glabrous or slightly hairy; ligule short, fimbriate; blade linear-acuminate, 16–32 (–50) × 1.5–2.5(–4) cm, midrib prominent, slightly rough. The inflorescence is a spike-like panicle 5–30 × 1–2(–5) cm, erect or pendulous, continuous or interrupted at the base; the rachis is ribbed and hairy; the lateral branches are short, bearing 6–12 spikelets. The spikelets are almost sessile, subtended by 1–3 bristles up to 1.5 cm long, elliptical, usually about half as long as the bristles. Its fruit is a caryopsis (grain), which is enclosed in coloured hulls with the colour depending on the variety. The grain is broadly ovoid, up to 2 mm long. The colour of the grain varies from pale yellow to orange, red, brown, or black. Generally, foxtail millet seeds are not dormant. The 1000-seed weight is about 2 g. Foxtail millet has a short vegetation crop; total crop duration is 80–120 days, although some cultivars only need 60 days to mature. Foxtail millet is largely self-pollinating with an average outcrossing rate of 4%; natural hybrids between wild and cultivated types occur. Foxtail millet has largely lost the ability of natural seed dispersal and shows a tendency toward uniform plant maturity (Hermuth *et al.*, 2016).

It is an annual grass with erect and robust culms. It grows up to the height of 60–150 cm. Leaves are 20–40 cm long and 1.5–3 cm wide with lanceolate shape. Leaf sheaths are small, glabrous or pubescent and 1–3 mm. Leaf lamina is dense, erect or pendent, lobed and 6–40 × 0.5–5 cm. It has elliptic, ovate or subglobose spikelets of 2–3 mm (SM, 2017). 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 in height with slim, erect, and leafy stems. 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. 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. 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 meter or in field conditions in temperate or tropical regions. 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 (Singh *et al.*, 2017).

Foxtail millet has small caryopses with an average 1000 kernel weight of only 2 g of about 2 mm length. The kernels are enclosed in thin outer glumes, which are removed during threshing. The color of the caryopses can be white, red, yellow, brown, or even black. The surface of the glumes of foxtail millet is covered with small peaks arranged symmetrically. The pericarp is thin with two characteristic epidermal layers firmly compressed to each other and contains large numbers of starch granules that disappear after maturation. The testa collapses and is reabsorbed during grain maturation. Foxtail kernels have a one-layered aleurone, which accommodates a dense cytoplasm. This layer completely surrounds the endosperm and germ and is composed of cells that are 25–50 μm in length with protein bodies and distinctive spherosomes. Similar to other millets, the

starch granules are angular and spherical in the corneous and floury endosperm areas, respectively. The size of the starch granules ranges from 0.8 to 11.8 μm. The protein bodies are concentrated in the peripheral cells of the endosperm, becoming more scattered and less frequent toward the inside. The protein bodies are spherical, 1–2 μm in diameter, with a subtle internal structure consisting of alternating light and dark concentric layers. The germ also contains protein bodies but does not have any inclusions. The scutellum consists of irregularly shaped cells and appears in the form of two wing-like expansions. Upon maturation, the chalazal region of the embryo becomes a part of the scutellum. Unlike other cereals, the embryo lacks a distinctive epiblast (Serna-Saldivar and Espinosa-Ramírez, 2019). In botany, a caryopsis (PL caryopses) is a type of simple fruit—one that is monocarpellate (formed from a single carpel) and indehiscent (not opening at maturity) and resembles an achene, except that in a caryopsis the pericarp is fused with the thin seed coat. The caryopsis is popularly called a grain and is the fruit typical of the family Poaceae (or Gramineae). Considering that the fruit wall and the seed are intimately fused into a single unit, and the caryopsis or grain is a dry fruit, little concern is given to technically separating the terms *fruit* and *seed* in these plant structures. In many grains, the "hulls" to be separated before processing are flower bracts.

The stem produces an inflorescence terminally. There is a very quick transition period from vegetative growth to flower- development. The inflorescence is a dense, cylindrical terminal spike borne on a thin and very short pedicel with short side branches bearing spikelets and bristles. The shortened side branches are called secondary clusters or lobes. The panicle is 8–32 cm long and 2–4 cm in diameter often arching towards the tip. The spikelets are glabrous, elliptic to obovate and about 2 cm long. Each spikelet consists of a pair of glumes that embrace two minute flowers (about 1 mm in length); the lower one sterile and the upper one bisexual and fertile, with three stamens and a long oval smooth ovary with two long styles, that terminate in a brush like stigma. Spikelets are generally in clusters of 40 or 50 (called lobe). There are 1–3 bristles at the base of each spikelet. The length and density of these bristles on the panicle depend on the genotype. When first initiated, spikelets and bristles appear to be paired and, if all spikelets grew to maturity, the numbers of spikelets and bristles would be approximately equal. However, a number of spikelets cease development and persist as tiny rudiments. The panicle can be compared to a primary cluster made up of several secondary clusters (Sc), small rounded spikes. The second order clusters are made up of third-order clusters (Tc) and are arranged in a helicoidal disposition on the panicle. The third order clusters consist of a few spikelets (up to 10). The secondary clusters are generally sparse at the bottom of the inflorescence and densely aggregated at the top. The anthers are yellow or white, ovary surmounted by two long styles and feathery stigmas. The lodicules are two in number. The grain is oval in shape, shiny, 2 mm in length, tightly enclosed within the thickened lemma and palea. At maturity, grain is encased in a thin, papery hull which is easily removed after threshing. The seed coat and husk of foxtail are generally of single entity with glossy appearance. The grains are with outer husk, which needs to be removed in order to be used. Seed colour varies greatly between genotypes, and usually yellowish, cream to orange or yellow brown to black in colour (Hariprasanna, 2020).

Foxtail millet is one of the oldest cultivated cereal grain and the most economically important species of the *Setaria* genus. Foxtail millet is usually grown for its grain (see the Foxtail millet grain datasheet) but it is also cultivated as a fodder plant. Foxtail millet is an erect annual grass, fast-growing, leafy and tufted, 90–220 cm high. It has a dense root system of thin adventitious roots. Its stems are erect, slender and tiller from the base. The leaves are alternate with lanceolate and serrated blades, 15–50 cm long and 0.5–4 cm broad. The inflorescence is an erect or pendulous spike-like bristly panicle, 5–30 cm long x 1–5 cm wide, bearing between 6 and 12 spikelets. There are many wild and cultivated types of *Setaria italica*, which are interfertile. Wild types are annual weeds (green foxtail millet) that are very common in temperate areas. Cultivated types differ in height, habit, structure of

inflorescences, number and colour of grain. *Moharia* cultivars are high-tillering (up to 50 culms) with more or less erect inflorescences. They are grown in Europe, USA and in Southwestern Asia, mainly for fodder. Maxima cultivars have between 1 and 8 unbranched culms with large inflorescences. They are cultivated in Russia and Asia. Indica cultivars are intermediate in terms of number of tillers and in inflorescence size (Heuzé *et al.*, 2020). Foxtail Millet is an annual with rather stiff and erect stems, ordinarily from two to four feet high, but sometimes reaching a height of six feet or more. The leaves arc-broad and somewhat similar in size and texture to those of Common Millet (*Pennisetum glaucum*). From the latter, however, this plant is easily distinguished, even when very young, by its lack of hairiness. The inflorescence is a contracted panicle, often nodding at the top; on account of its short branches it resembles a spike. Its lower branches, as a rule, are not so close together as the upper ones. The spikelets are crowded and mixed with stiff bristles, the latter representing branches on which no spikelets are developed. These bristles are generally long and often reddish or purplish. They give the panicle the appearance of a foxtail, which is the common name for cultivated millets belonging to the genus *Setaria*. Each spikelet contains only one flower with a yellow pistil. The seed varies in size. It is always smaller than the seed of Common Millet, but is of the same general shape, though the inner side is more decidedly flat. The colour varies with the variety, ranging from orange and yellow to grey and black. Sometimes different coloured seeds are found in the same variety. This is especially the case in Hungarian Grass, the seed of which varies from pale yellow to black; seeds of widely different colour may occur in the same plant and even in the same head. So far as is known, no satisfactory explanation of this fact has been offered. It may be the result of cross-fertilization and thus correspond to the similar phenomenon observed in corn (Chestofbooks, 2021).

Foxtail millet is an annual grass with slim, vertical, leafy stems which can reach a height of 120–200 cm. The seedhead is a dense, hairy panicle 5–30 cm long. The small seeds, around 2 mm in diameter, are encased in a thin, papery hull which is easily removed in threshing. Seed color varies greatly between varieties (Wikipedia, 2023). Foxtail millet is an annual plant with rather stiff and erect stems, ordinarily from 60-120 cm high, but sometimes reaching a height of 2 m or more. The leaves arc is broad and somewhat similar in size and texture to those of *Panicum milliaceum*. From the latter, however, this plant is easily distinguished, even when very young, by lack of hairiness. The inflorescence is a contacted panicle, often nodding at the top; on account of its short branches it resembles a spike. Its lower branches, as a rule, are not so close together as the upper ones. The spinklets are crowded and mixed with stiff bristles, the latter representing branches on which no spinklets are developed. These bristles are generally long and often reddish or purplish. They give the panicle an appearance of a foxtail, which is the common name for cultivated millets belonging to the genus *Setaria*. Each sprinklet contains only one flower with a yellow pistil. The seed head is dense, hairy panicle 5 to 30 cm long. The small seeds, around 2 mm (less than 1/8th inch) in diameter, are encased in a thin, papery hull which is easily removed in threshing. Seed colour varies greatly between varieties (Fig. 3) (Rutuja, 2023). Millet is a leafy, slender, vertical-stemmed annual that reaches 120-200 cm in height. The seed head is a dense, hairy panicle 5 to 30 cm long. The small seeds, about 2 mm in diameter, are enclosed in a thin papery shell and are easily removed during threshing. Seed color varies greatly depending on the variety (Academic, 2023). Foxtail Millet is an annual with rather stiff and erect stems, ordinarily from two to four feet high. but sometimes reaching a height of six feet or more. The leaves arc broad and somewhat similar in size and texture to those of Common Millet (*Pennisetum glaucum*). From the latter, however, this plant is easily distinguished, even when very young, by its lack of hairiness. The inflorescence is a contracted panicle, often nodding at the top; on account of its short branches it resembles a spike. Its lower branches, as a rule, are not so close together as the upper ones. The spikelets are crowded and mixed with stiff bristles, the latter representing branches on which no spikelets are developed. These bristles are generally long and often reddish or purplish.

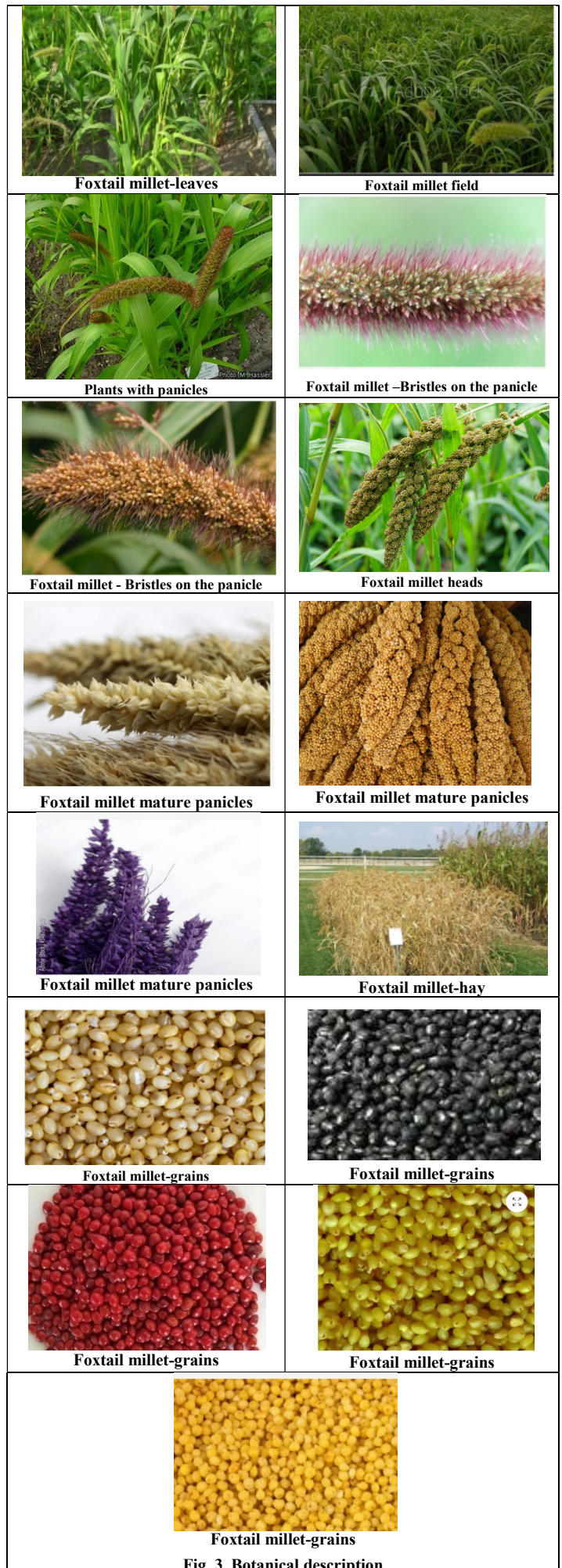


Fig. 3. Botanical description

They give the panicle the appearance of a foxtail, which is the common name for cultivated millets belonging to the genus *Setaria*. Each spikelet contains only one flower with a yellow pistil (Plant guide, 2023).

Floral biology

The flowers below the apex of the head begin to open when about three-fourth of the head emerges out of the sheath. Flowering proceeds from the top to downward in the main spike. A head takes 8 to 16 days to complete flowering. A single floret remains open for about 30 minutes, and it may take about 80 minutes for complete blooming, which is hastened by high temperatures and low humidity. During pollination tips of stigmatic branches and the anthers protrude through the slit between the incurved edges of the palea. The stigmatic branches emerge first followed by emergence of anthers. The anther after emergence starts dehiscing by longitudinal slits from the top to bottom. As the glumes began to spread, the stigmas and the anthers developed and pushed out of the slit between the incurved edges of the palea. The feather like stigmas were first to emerge, but were quickly followed and overtaken by the anthers. Sometimes, some anthers remained adhered in the curved edges of the palea. This pattern is generally associated with round shaped flowers or moisture deficient soil. In general, the anthers shed pollen after they are fully extruded outside the glumes. After dehiscence, the glumes began to close, leaving the shriveled anthers and the tip of the stigmas outside. After pollination, the lodicules shrink and glumes begin to close. Anthesis in foxtail millet generally takes place near midnight and in the morning, but varies significantly with the environment. Most of the flowers opens during the midnight and between 8-10 a.m. The duration for an ear head to complete its flowering varies from 10-15 days. Maximum number of floret opens on sixth day of emergence. Humidity and temperature are the main factors that affect pollination (Fig. 4-5) (Gupta *et al.*, 2012).

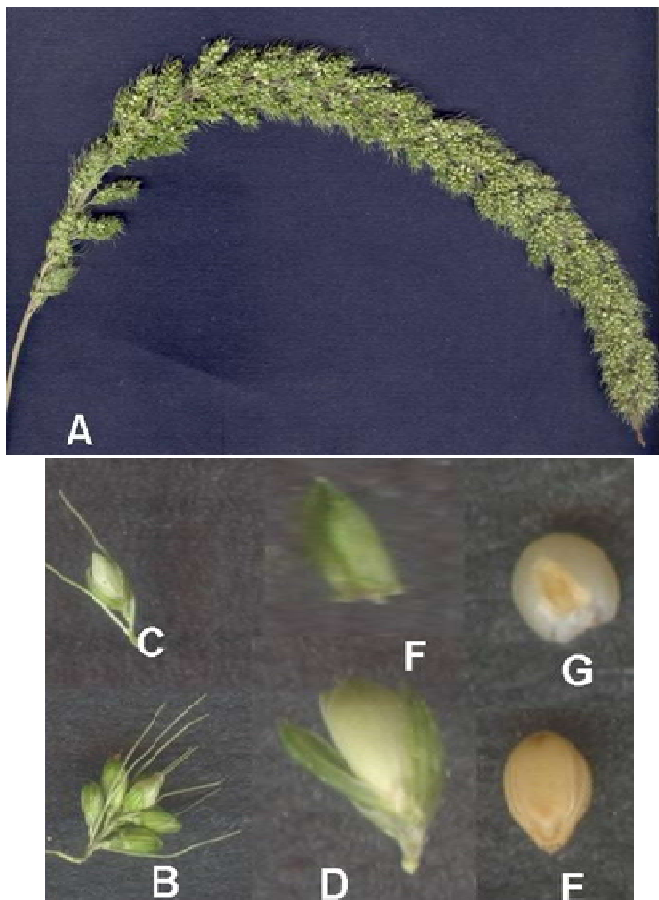


Fig. 4. Foxtail millet inflorescence and its parts **A.** Inflorescence; **B.** Spikelets cluster; **C.** Subtended spikelet; **D.** Opened spikelet; **E.** Outer glume; **F.** Grain enclosed in lemma and palea; **G.** Grain

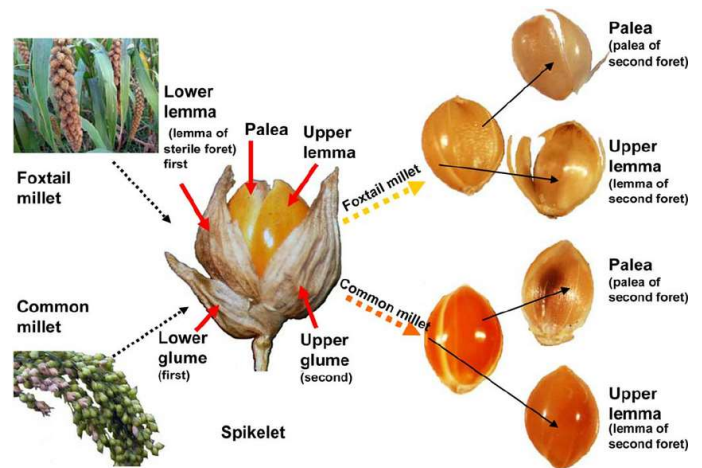


Fig. 5. Parts of a flower

Foxtail millet is largely a self-pollinating species, with cross pollination averaging about 4%. Anthesis in foxtail millet generally takes place near midnight and in the morning, but varies significantly with the environment. The rate of anthesis is generally favoured by low temperature and high humidity. In general, there is no anthesis during day time. Morphology and anthesis behaviour make foxtail millet one of the most difficult species to cross pollinate. The spikelets below the tip of the panicle begin to open when about three-fourth of the panicle emerges out of the sheath. Flowering proceeds from the top to downward in the main spike. A panicle takes 6-10 days to complete flowering. A single floret remains open for about 30 minutes, and it may take about 80 minutes for complete blooming, which is hastened by high temperatures and low humidity. During pollination tips of stigma and the anthers protrude through the slit between the incurved edges of the palea. The stigmatic branches emerge first followed by emergence of anthers. The anther after emergence starts dehiscing by longitudinal slits from the top to bottom. As the glumes begin to spread, the stigma and the anthers are pushed out of the slit between the incurved edges of the palea. The feather like stigmas are first to emerge, but quickly followed and overtaken by the anthers. Sometimes, some anthers remain adhered in the curved edges of the palea, which is generally associated with round shaped spikelets or moisture deficiency. In general, the anthers shed pollen after they are fully extruded outside the glumes. After dehiscence, the glumes begin to close, leaving the shriveled anthers and the tip of the stigmas outside. After pollination, the lodicules shrink and glumes begin to close. Anthesis in foxtail millet generally takes place near midnight and in the morning, but varies significantly with the environment. Most of the flowers opens during the midnight and between 8-10 a.m. The duration for a panicle to complete its flowering varies from 8-12 days. Maximum number of floret opens on sixth day of emergence. Humidity and temperature are the main factors that affect pollination (Hariprasanna, 2020).

Emasculation and hybridization

The difficulty in making crosses artificially and lack of an efficient crossing technique have resulted in a very limited number of genetic studies and limited improvement of foxtail millet. The minute size of spikelet makes it difficult for any manipulation with respect to hand emasculation. The technique involved removal of anthers as soon as anthesis starts in the early morning after isolation of female parent. The bristles of male and female parent were excised gently with a pair of scissors first. Emasculation was done when the first anther had just emerged and before the pollen sacs had burst. The three anthers were carefully removed using a fine forceps with the help of magnifying glasses. If the anthers were not fully pushed out, the anthers were removed by gently inserting the forceps at each side of the palea and pushing the anther out quickly. The emasculated flower was marked immediately for identification. After emasculation is over, all the unmarked flowers were removed and panicle was covered with a butter paper bag. Pollination was immediately done by bringing the emasculated panicle below the male panicle that has started shedding

pollen and covering both the panicles together. The pollen shed from the male panicle provides opportunity for fertilization of emasculated spikelets. The panicles were shaken together gently for 2 days during the period of anthesis. As the stigmas remain outside the glumes and are receptive for 48 h the shaking process provides opportunity for fertilization. On the 3rd day the male panicle was carefully removed and emasculated panicle was carefully checked for any floret that may have developed later. Such florets were removed by identifying the absence of mark. The female panicle was covered again and maintained till maturity (Siles et al., 2001). The most commonly followed method to make crosses is hot water emasculation followed by contact method. The emasculation is done during the evening hours. In this select the female panicle which has just started anthesis at the tip and cut the tip portion. Select only a few lobes containing well developed spikelets which will open the next day. Remove the remaining lobes from the bottom as well on the other side of the selected spikelets using a pair of scissors. Thin out the spikelets from the selected lobe in case of a dense lobe. Also remove the bristles which will prevent free flow of pollen. Dip the female panicle in hot water maintained at 48-50 °C for 2 minutes. Then take out the panicle and cover with a butter paper bag. The pollination is done in the next morning following contact method. Select the male panicle which will be opened and cut with long stalk from the plant. Bring this panicle to the emasculated panicle and tie the whole male panicle with female panicle using twine. Cover with butter paper bag. Immerse the cut end of the male panicle in water kept in a bottle/test tube to prevent drying of male panicle. Natural cross pollination takes place in 2 to 5 days. A gentle shaking can be given in the morning hours to promote pollen dispersal. Alternatively, if the parents are grown in pots the pots can be brought together and male panicle and hot water treated female panicle can be tied together and covered with butter paper bag. After 5 days when the anthesis will be over the male panicle can be removed. At maturity carefully harvest the seeds from emasculated panicle. Contact method can also be followed in the field by planting the parents in paired rows and adjusting the sowing dates for flowering synchronization (Hariprasanna, 2020). The foxtail millet is highly autogamous and the extent of out crossing varies from 1.4- 4%. Natural crossing occurs between the cultivated and the wild taxa of foxtail millet, derivatives of such hybrids are obnoxious weeds. In general, tetraploids are more vigorous but colchicines induced auto-tetraploids in foxtail millet were smaller, late in flowering and had a two-fold reduced level of fertility. However in another study 20% increase in grain weight was observed in polyploids, but the total grain yield decreased by 46%. A genetic male sterile line controlled by dominant gene 'Ch A' and photoperiod sensitive male sterility are being used in hybridization program in China (Gupta et al., 2012).

GENETICS AND CYTOGENETICS

As with some other cereals the waxy gene contributes to glutinousness. The wild relative *Setaria viridis* provides genetic resources useful for foxtail breeding (Wikipedia, 2023). Foxtail millet is one of the oldest domesticated diploid C4 Panicoid crops having a comparatively small genome size of approximately 515 Mb, short life cycle, and inbreeding nature (Lata et al., 2013). Foxtail millet is a member of the subfamily Panicoideae and the tribe Paniceae with chromosome number of $2n = 2x = 18$ (AA). It is an important ancient crop of dry land agriculture, grown since >10,500 years ago in China. The green foxtail, *Setaria viridis* ($2n = 2x = 18$, AA), is a wild ancestor of cultivated foxtail millet. The genus *Setaria* is organized into three gene pools based on observations drawn from interspecific hybridization and hybrid pollen fertility. The primary gene pool is composed of cultivated foxtail (*S. italica*) and its putative wild ancestor *S. viridis*. The secondary gene pool contains *Setaria adhaerans* ($2n = 2x = 18$) and two allotetraploids *Setaria verticillata* and *Setaria faberii* ($2n = 4x = 36$). The tertiary gene pool contains *Setaria glauca* (or *Setaria pumila*, $4x$ to $8x$) in addition to many other wild species. Morphological and molecular studies on cultivated and green foxtail revealed large genetic diversity (Vetriventhan et al., 2016). The genome of *S. italica* and *S. viridis* (green foxtail) is designated as AA genome with $2n = 2x = 18$. 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*. *Setaria grisebachii* from Mexico has been identified as CC genome diploid species. *Setaria queenslandica* is the only autotetraploid (AAAA genome) species in genus *Setaria* whereas other polyploid species such as *Setaria pumila* and *Setaria pallidifusca* do not contain the AA genome (Singh et al., 2017). Foxtail millet, subfamily Panicoideae, tribe Chloridoideae, is diploid with nine chromosomes ($2n = 18$). It is, however, closely related to tetraploid and polyploid species of *Setaria*. Furthermore, cultivated foxtail millet will cross with its wild relative *Setaria italica* subsp. *viridis* (synonym *Setaria viridis*; green foxtail) to produce fertile hybrids. It has a small genome, ca. 423 Mbp. Foxtail millet can be classified into three or four races: *maxima*, *moharia*, *indica*, and *nana* (Taylor and Emmambux, 2019). So far, five genomes, namely foxtail millet, finger millet, proso millet, teff, and Japanese barnyard millet, have been sequenced, and genome of foxtail millet is the smallest (423-510 Mb) while the largest one is finger millet (1.5 Gb). Recent advances in phenotyping and genomics technologies, together with available germplasm diversity, could be utilized in small millets improvement. This review provides a comprehensive insight into the importance of small millets, the global status of their germplasm, diversity, promising germplasm resources, and breeding approaches (conventional and genomic approaches) to accelerate climate-resilient and nutrient-dense small millets for sustainable agriculture, environment, and healthy food systems (Vetriventhan et al., 2020).

GENETIC DIVERSITY

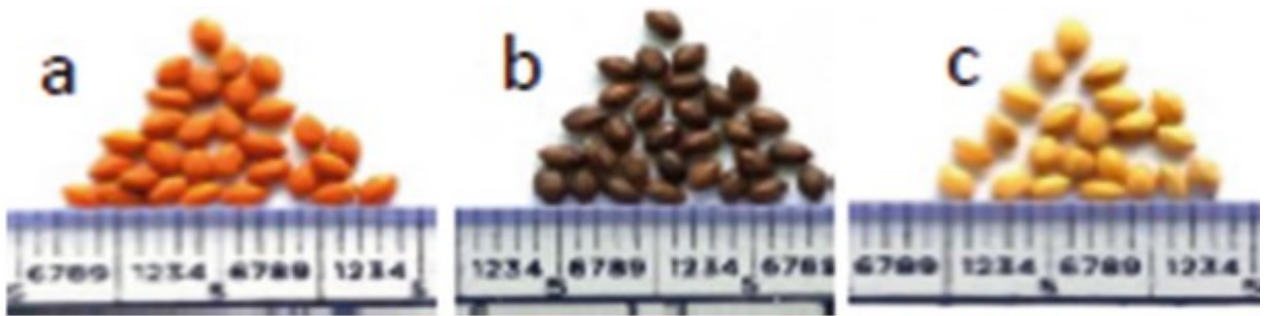
Foxtail millet is very variable and numerous cultivars exist, differing in time to maturity, plant height, size, habit and structure of inflorescence, number, colour and length of bristles, and colour of grain (Brink, 2006). Fruit a caryopsis (grain), broadly ovoid, up to 2 mm long, pale yellow to orange, red, brown or black, tightly enclosed by lemma and palea (Brink, 2006). Cultivated types differ in height, habit, structure of inflorescences, number and colour of grain. Moha cultivars are high-tillering (up to 50 culms) with more or less erect inflorescences. They are grown in Europe, USA and in Southwestern Asia, mainly for fodder. Maxima cultivars have between 1 and 8 unbranched culms with large inflorescences. They are cultivated in Russia and Asia. Indica cultivars are intermediate in terms of number of tillers and in inflorescence size (Heuzé et al., 2020). The seed head is dense, hairy panicle 5 to 30 cm long. The small seeds, around 2 mm in diameter, are encased in a thin, papery hull which is easily removed in threshing. Seed colour varies greatly between varieties (Rutuja, 2023). The seed varies in size. It is always smaller than the seed of Common Millet, but is of the same general shape, though the inner side is more decidedly flat. The colour varies with the variety, ranging from orange and yellow to grey and black. Sometimes different coloured seeds are found in the same variety. This is especially the case in Hungarian Grass, the seed of which varies from pale yellow to black; seeds of widely different colour may occur in the same plant and even in the same head. So far as is known, no satisfactory explanation of this fact has been offered. It may be the result of cross-fertilization and thus correspond to the similar phenomenon observed in corn (Chest of books, 2023) (Fig. 6-11).

The genetic diversity of a world collection of foxtail millet strains (*Setaria italica*) and some samples of wild populations (*Setaria viridis*) was studied by means of electrophoresis on five enzymes (10 loci) Est, Acph, Got, Mdh, Pgd. In spite of an overall limited polymorphism, the diversity appeared to be clearly regionalized. The wild populations collected in France and China introduced new genetic variability to the cultivated forms. However, the interregional diversity within both species was greater than the between species (*S. viridis/S. italica*) diversity (Jusuf and Pernes, 1985). A total of 23 381 foxtail millet landraces of Chinese origin were analysed for seven qualitative traits and four quantitative traits. The Shannon-Weaver diversity index was used to estimate the phenotypic diversity of each characteristic on the basis of administrative provinces and ecogeographical regions.



Fig. 6: Genetic diversity in Foxtail millet: A-D. Variation in anther color; E-H. Panicle density variation; I-N. Husk color variation; O-R. Bristles variation; S-V. Panicle attitude variation

Panel 1



Panel 2



Panel 3



Panel 4



Panel 5



Panel 6

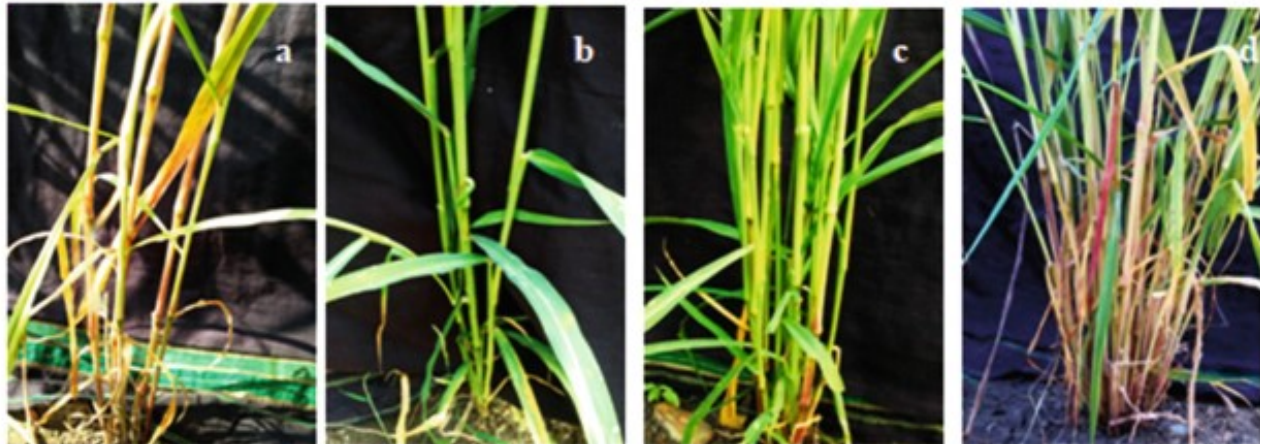


Fig. 7. Genetic diversity of Foxtail millet

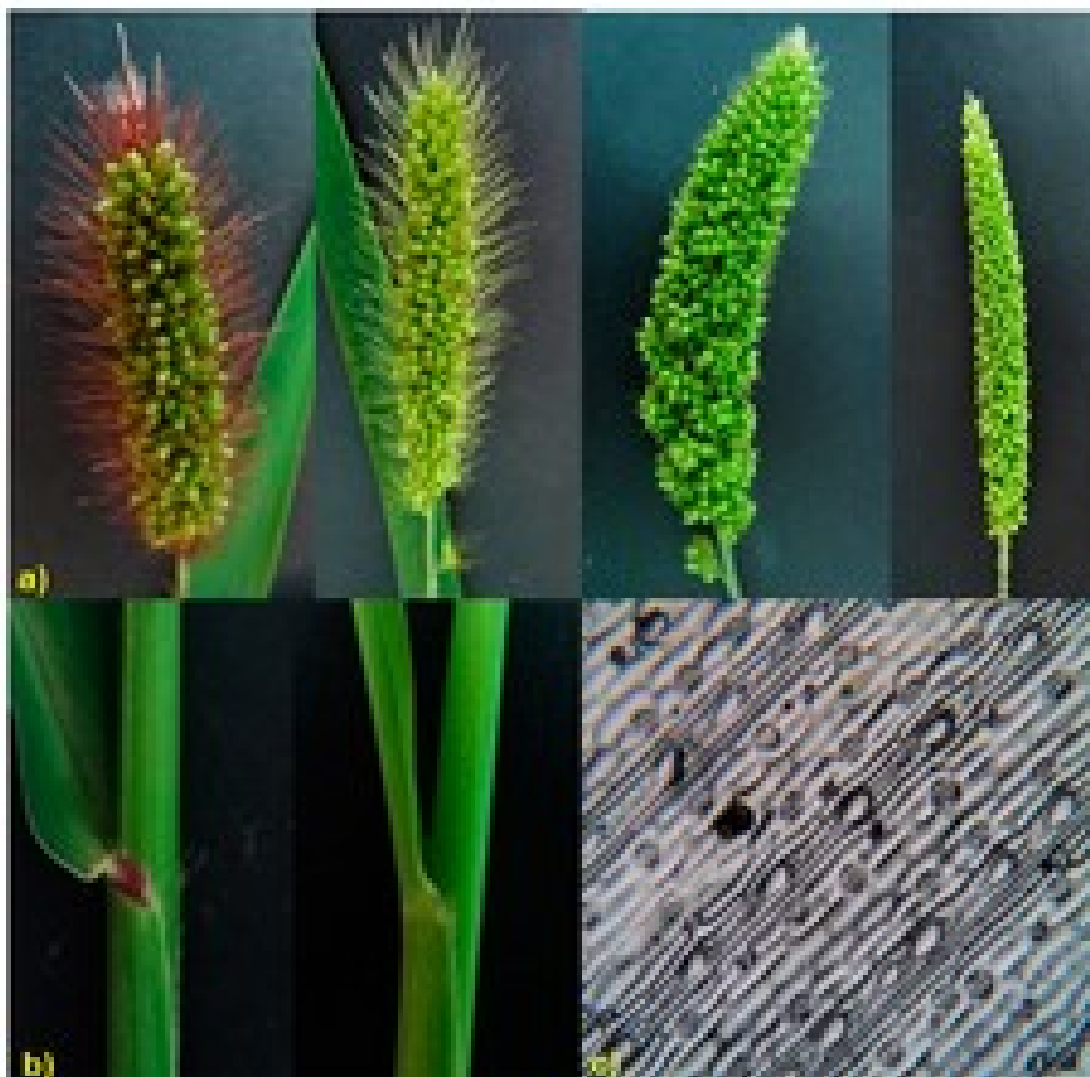


Fig. 8. Genetic Diversity: A. Panical variation, B. Leaf sheath color variation, C. Stomatal and epidermal cell variation



Fig. 9. Genetic diversity: Panicle color



Fig. 10. Variability for color, size and shape of panicles in Foxtail millet



Fig. 11. Genetic Diversity for seed color, shape and size in Foxtail millet

Hierarchical analysis of variance indicated that most of the variation was due to differences among characteristics. Only the diversity indices for leaf color of seedlings, starch composition and 1000-grain weight showed significant differences among regions. In relative terms, a greater genetic divergence was found in some provinces of southern China, where foxtail millet is not a major crop (Yu Li *et al.*, 1996).

China is among the countries that have the most severe water deficiency. Due to its excellent drought tolerance, foxtail millet has become one of the important cereal crops in China. Information on genetic diversity and population structure of foxtail millet may facilitate effective use of limited genetic resources in breeding programs. In this study, a selected panel of 128 accessions was screened with 79 simple sequence repeat (SSR) markers to investigate genetic diversity and population structure of foxtail millet.

The panel was selected from 3356 germplasm collections from three major ecological areas of China: North, Northwest, and Northeast China. The mean genetic diversity was 0.75 and the mean polymorphism information content (PIC) was 0.72, indicating a high level of genetic diversity across the panel. Structure analysis identified six groups, which matches with their pedigree information, in general, but not with their geographic origins. Germplasm in Group 2 (G2) have unique geographic origins and pedigrees, which is different from other five groups; thus, crosses of accessions in this group to accessions from other groups are more likely to generate expected recombination for developing both conventional and hybrid cultivars (Zhengli Liu *et al.*, 2011). Foxtail millet core collection consisting of 155 accessions was evaluated at three environments for 12 qualitative and 13 quantitative traits to study the phenotypic diversity and to identify trait specific accessions. Foxtail millet core collection was also molecularly profiled using 84 SSR markers to study molecular genetic diversity, population structure and to identify SSR markers associated with the agronomic traits. In REML analysis variance due to genotypes (σ^2_g) and genotype \times environment (σ^2_{ge}) were significant for all the 13 quantitative traits. On the basis of phenotypic dissimilarity between pair of accessions, ten pairs of most diverse accessions were identified for breeding program for the developing high yielding cultivars with a broad genetic base and for the development of mapping populations. On the basis of pooled BLUPs (Best Linear Unbiased Predictors) of three environments, we have identified trait specific accessions for economically important traits such as yield and its traits contributing to yield (15 accessions for each trait). These accessions could be used in recombination breeding to develop cultivars with desirable combination of traits. The SSR markers detected a total of 1,356 alleles with an average of 16.14 alleles per locus. Of these, 368 were rare alleles; 906 common alleles; and 82 the most frequent alleles. Sixty one unique alleles which were specific to a particular accession and useful for germplasm identification were also detected. The genetic diversity of foxtail millet in this study was correlated well with racial classification and the race *indica* showed greater genetic distance from the *maxima* and *moharia*. Ten pairs of genetically most diverse accessions were identified. Large molecular variation observed in core collection could be utilized effectively for selection of diverse parents for breeding cultivars and development of mapping populations.

Mantel test showed significant correlation between phenotypic and molecular dissimilarity matrix. The STRUCTURE analysis provided the evidence for the presence of four subpopulations. The mixed linear model (MLM) was used and the number of significant marker trait association was 130 in E1, 69 in E2 and 106 in E3 at $P \leq 0.05$, whereas only 49 in E1, 23 in E2 and 61 in E3 were found to be highly significant MTAs at $P \leq 0.01$. In pooled BLUPs of three environments, a total of 108 MTAs were detected at $P \leq 0.05$. Of these 18 SSR markers showed 37 significant associations at $P \leq 0.01$ with yield and yield contributing traits. Fifteen MTAs, that occurred in all three environments and overall in pooled data were identified as stable. Our research provided a first report of association study for yield and yield contributing traits in foxtail millet using SSR markers. The results from this research also demonstrated the use of core collection as association mapping panel to disclose marker-trait associations in foxtail millet for yield traits that could lead to effective utilization of ex-situ conserved genetic resources (Vetriventhan, 2011). *Setaria italica* (L.) P. Beauv. is a model plant that attracts international attention, which is the second most widely cultivated species of millet, especially in East Asia. It has the longest history of cultivation among the millets, having been grown in China since sometime in the sixth millennium BC. It also has been a main crop of the indigenous people of Taiwan for a long time. However, insufficient researches had been conducted about the foxtail millet germplasm in Taiwan. To assess the genetic diversity of millet population, a total of 324 landraces of foxtail millet were collected from around Taiwan, and four years of field researches were conducted for agronomic traits observation. The genetic diversity of the millet population was measured using 33 agronomic traits and 40 microsatellite markers. Average number of alleles (2.4), highly polymorphic information

content (PIC) (0.381), observed heterozygosity (0.190) and expected heterozygosity (0.354) were shown. Thirty-five SSR markers showed significant deviation from Hardy-Weinberg equilibrium in 324 landraces and all these markers had low null allele frequencies. Analysis with the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) method and Principal Component Analysis (PCA) revealed that the 324 landraces could be divided into three groups that coincided with the geographical areas, including northern Taiwan, central Taiwan, and southern Taiwan, which account for close relationship between crop distribution and human activities. Agronomical analyses with a plant height of 80.6 to 155.2 cm, spike length of 7.5 to 28.9 cm and growth periods of between 141 and 178 days had showed that there was enough variation to create promising lines for breeding programs. This study not only provides a complete foxtail millet germplasm from Taiwan but also demonstrates that the Taiwanese foxtail millets are very diverse and can be useful for selective breeding of specific traits and in enhancing the genetic base of breeding programs in the future (Heng-Sheng Lin *et al.*, 2012).

An investigation was carried out to assess nature and magnitude of genetic variability for productivity related traits in foxtail millet germplasm collections during rainy and post rainy season. The analysis of variance revealed the presence of highly significant differences for all characters, indicating collections under study were genetically diverse for all the traits. Significant variation was recorded among the genotypes for various yield and yield contributing traits studied. In both the seasons high values for phenotypic coefficient (PCV) and genotypic coefficient (GCV) was recorded for number of tillers per plant, followed by panicle weight per plant, straw weight and grain yield per plant. Moderate GCV and PCV for characters *viz.*, days to flowering and panicle length. The low GCV and PCV was recorded in days to maturity and plant height. The grain yield and its components *viz.*, days to flowering, number of productive tillers, panicle length, test weight, grain yield per plant and straw yield per plant exhibited high genetic advance as per cent of mean coupled with high estimates of h^2_b indicating that, the variations are attributable to high level of heritable variation and selection would be effective for improvement of these traits (Brunda *et al.*, 2014). An investigation was carried out to know the genetic diversity among the genotypes foxtail millet during rainy season. Experimental material consisted of 78 genotypes evaluated in Randomized Complete Block Design with three replication at Agricultural Research Station Nipani, University of Agricultural Sciences, Dharwad during rainy season 2013. The extent of genetic diversity for yield and its attributing traits in the 78 genotypes of foxtail millet were studied. Observations were recorded for ten quantitative traits. On the basis of Mahalanobis D2 statistics these genotypes were grouped into seven clusters. The highest intra-cluster distance was recorded for cluster-III. The genotypes from cluster V may be crossed with those in cluster VII as they are more diverse. The clusters were highly divergent this suggests the presence of wide diversity between these clusters. Therefore, genotypes from these clusters can be selected for hybridization programme to get desirable recombinants. The days to flowering have maximum contribution towards the genetic divergence followed by test weight and grain weight (Brunda *et al.*, 2015).

Foxtail millet is a crop of historical importance in some Asian and European countries. In this study, we selected the internal transcribed spacer (ITS) region of nuclear ribosomal DNA (nrDNA) as the DNA marker to analyze genetic diversity and relationships of 20 foxtail millet strains collected from three representative Asian countries, including China, Korea, and Pakistan. Due to the length limitation of the nrDNA ITS region, 17 typical variable nucleotide sites were only found, of which 4 sites belonged to insertion, 3 sites deletion, and 10 sites substitution. According to the result of sequence alignment, strains were grouped clearly with the relevant of collected geographical region. Based on the sequence similarity and nucleotide variation, one Main China Group (MCG) and one Main Korea Group (MKG) occurred, and the strains from Pakistan were found to be close to MKG, considered to be originally transmitted from Korea and spread to Pakistan. Certain genetic diversity between strains from

Pakistan and Korea were recognized as long-time environment evolution and adaptation. Among strains from Korea, K2, K3, K4, and K5 showed nearer phylogenetic relationship to MCG, considered as Chinese populations. All strains from China showed relatively near phylogenetic relationship with each other, supporting the statement that China is one of origin areas. The result also suggested that there was no introduced strain found in the Chinese strains investigated in this study. This work would provide more sequence sources and help clearer strain distinguishing, genetic diversity and phylogenetic relationship of foxtail millet (Sun *et al.*, 2016). Foxtail millet is a crop of historical importance in some Asian and European countries. In this study, we selected the internal transcribed spacer (ITS) region of nuclear ribosomal DNA (nrDNA) as the DNA marker to analyze genetic diversity and relationships of 20 foxtail millet strains collected from three representative Asian countries, including China, Korea, and Pakistan. Due to the length limitation of the nrDNA ITS region, 17 typical variable nucleotide sites were only found, of which 4 sites belonged to insertion, 3 sites deletion, and 10 sites substitution. According to the result of sequence alignment, strains were grouped clearly with the relevant of collected geographical region. Based on the sequence similarity and nucleotide variation, one Main China Group (MCG) and one Main Korea Group (MKG) occurred, and the strains from Pakistan were found to be close to MKG, considered to be originally transmitted from Korea and spread to Pakistan. Certain genetic diversity between strains from Pakistan and Korea were recognized as long-time environment evolution and adaptation. Among strains from Korea, K2, K3, K4, and K5 showed nearer phylogenetic relationship to MCG, considered as Chinese populations. All strains from China showed relatively near phylogenetic relationship with each other, supporting the statement that China is one of origin areas. The result also suggested that there was no introduced strain found in the Chinese strains investigated in this study. This work would provide more sequence sources and help clearer strain distinguishing, genetic diversity and phylogenetic relationship of foxtail millet (Sun *et al.*, 2016).

In China, the systematic collection of foxtail millet germplasm from the 1950s to the 1980s resulted in the compilation of 27,059 accessions in the Chinese Gene Bank. There are approximately 15,000 additional foxtail millet accessions maintained in other gene banks in India, Japan, Korea, the United States of America, Russia, and in other countries. Evaluations of the Chinese and Indian accessions indicate that foxtail millet is morphologically and genetically highly diverse, especially in China (Diao and Jia, 2017). Drawing upon the serious food insecurity issues and continually growing impacts of climate change on livelihood, diversity sourcing of climate-resilient, nutritionally rich crops like foxtail millet through diversity assessment and on-farm evaluation could be a reliable avenue to meet farmer's need and improve food security in the extremely mountainous agro-ecology of Nepal and elsewhere. In context of meager research on foxtail millet in Nepal, we conducted on-farm diversity assessment studies of 27 Nepalese foxtail millet landraces in 2015. Subsequently, we identified 8 locally adaptable and robust foxtail millet genotypes based on the inferences of diversity block trial and evaluated them under Humla and Jumla conditions in 2016 for sourcing end-user preferred varietal diversity. Our studies revealed existence of marked diversity among the Nepalese foxtail millet accessions, which could be effectively utilized for crop improvement. Kalo Kaguno, Seto Kaguno, Aule Kaguno, and CO1896 were found to be superior yielders in descending order while CO5644 and CO5647 were substantially found early maturing. Apart from acknowledging the potentiality of these genotypes as promising parents, we encourage deployment of the sourced diversity through (Yadav *et al.*, 2018).

The extent of genetic variability for nutritional traits in the 78 genotypes of foxtail millet were studied. The parameters were analyzed using both NIR and AAS. When all the nutritional parameters were studied it was found that there was no single genotype which was superior for all the parameters so we should select the genotype which is best for maximum number of characters. For protein content Ise 1468, GS 1000, Ise 375, GS 2099 and DHF

30, for crude fibre DHF 27, GS 2109 and DHF 2, for zinc DHF 6, DHF 7, DHF 3 and DHF 17, for iron PratapKagni, DHF 14, DHF 27, Ise 931 and DHF 26 recorded the highest nutrients composition compared to checks. The most promising genotypes for nutritional characters are DHF 2, DHF 5 and DHF 1. These three genotypes can be used as donors in a further plant breeding programme for the improvement of most of the characters (Brunda *et al.*, 2019). Due to the maternal inheritance of cytoplasm, using foxtail millet male sterile lines with a single cytoplasmic source as the female parent will inevitably lead to a narrow source of cytoplasm in hybrids, which may make them vulnerable to infection by cytoplasm-specific pathogens, ultimately leading to destructive yield losses. To assess cytoplasmic genetic diversity in plants, molecular markers derived from chloroplast DNA (cpDNA) have been used. However, such markers have not yet been applied to foxtail millet. In this study, we designed and screened nine pairs of polymorphic foxtail millet-specific primers based on its completely sequenced cpDNA. Using these primers, we analyzed the genetic diversity and cytoplasmic types of 130 elite foxtail millet parental lines collected in China. Our results revealed that the cytoplasmic genetic diversity of these accessions was low and needs to be increased. The parental lines were divided into four cytoplasmic types according to population structure analysis and a female parent-derivative evolutionary graph, indicating that the cytoplasmic types of elite foxtail millet lines were rather limited. A principal component analysis (PCA) plot was linked with the geographic and ecological distribution of accessions for each cytoplasmic type, as well as their basal maternal parents. Collectively, our results suggest that enriching cytoplasmic sources through the use of accessions from diverse ecological regions and other countries as the female parent may improve foxtail millet breeding programs, and prevent infection by cytoplasm-specific pathogens (Liu *et al.*, 2019). There is a great genetic diversity with a large number of germplasm collections maintained in countries like China, Japan, the USA and India. The crop is nutritionally superior as the grains contain high amounts of proteins, essential amino acids, minerals and vitamins and micronutrients like iron and zinc. Thus, foxtail millet can be useful for biofortification programs aimed at combating malnutrition. Foxtail millet is a relatively drought-tolerant crop and hence genomic interventions can be in place for genetic engineering for abiotic stress tolerance. Recent advancements in a draft genome sequence of this millet has spawned great enthusiasm in unraveling genetic and genomic intricacies, genome-wide molecular marker development, genomics-assisted breeding, identification and validation of stress-associated gene families. There have been great research efforts in the creation and facilitation of genomics databases. In this chapter, we present an overview of the importance, genetic diversity, potential and genomics interventions for foxtail millet improvement (Moharil *et al.*, 2019).

The present study aimed to investigate the genetic diversity of foxtail millet germplasm and select superior genotypes. To this end, 130 foxtail millet were studied under an augmented complete block design at Shahid Bahonar University Research Farm. Analysis of Variance was also carried out on the genotypes to determine the homogeneity of experimental field. The results proved that there were significant differences among the control genotypes regarding all their traits except for the plant lodging trait. Based on the results of stepwise regression for grain yield as a dependent variable in foxtail millet genotypes, the number of grains per panicle, the number of panicles, 1000-seed weight, and height respectively had the best efficiency as index traits in selecting genotypes. Based on the cluster analysis, the foxtail millet genotypes were classified into 5 groups. Comparison of the genotypes demonstrated that the genotypes S27 and S7, and cultivar Boston respectively, had the highest biological yield, and Bastan and genotype S27 had the highest grain yield among others. The current study revealed that genotypes S7 and S27 had a higher yield than Iran's only breed cultivar, namely Bastan, and therefore they can be used in breeding studies in order to produce superior cultivars (Aminizadeh and Mohammadi-Nejad, 2020). A total of 80 foxtail millet genotypes were evaluated for ten quantitative characters at MARS (Main Agricultural Research Station), UAS (University of Agricultural Sciences), Raichur during kharif 2018 to assess the

genetic diversity using Mahalanobis D2 statistic. The eighty genotypes were grouped into twelve clusters. The highest inter-cluster distance (6623.62) was observed between cluster-VIII and cluster-XII. The highest intra-cluster distance was observed in cluster VII (529.01). A high mean grain yield was observed in cluster-XI (59.72g). Plant height (46.96%) and grain yield (46.39%) have the highest contribution to the total divergence. The crosses between genotypes of the divergent clusters VIII and XII would manifest wide variability (Sri Gopi *et al.*, 2021).

BREEDING

Genetic resources: Large collections of foxtail millet germplasm are kept by the Institute of Crop Germplasm Resources (CAAS), Beijing, China (25,380 accessions), the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India (1528 accessions) and the All India Coordinated Minor Millet Project, University of Agricultural Sciences, Bangalore, India (1300 accessions). In Africa a collection of 451 foxtail millet accessions is kept at the National Dryland Farming Research Station, Machakos, Kenya. Resistance to blast and rust has been identified in germplasm collections (Brink, 2006). Foxtail millets are highly nutritious with diverse usage, well adapted to marginal lands, and mostly grown by resource-poor farmers. Worldwide more than 46,000 foxtail millet germplasm accessions have been preserved. Considerable variation exists for various biotic and abiotic stresses, and for quality including important agronomic traits. Entire genetic diversity of these crops has been captured in the form of core and minicore collections and is being used in genetic and genomic studies for identification of new sources of variation. Genomic resources are available in foxtail millet, while in finger millet these resources are being developed. Furthermore, use of genetic and genomic resources need to be accelerated to assist in developing improved cultivars of these crops (Vetriventhan *et al.*, 2016). The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) genebank is presently holding 1474 cultivated germplasm accessions from 23 countries. To utilize this diversity in research, a core collection (10% of the entire collection) was established using the taxonomic and qualitative traits data. The germplasm accessions were stratified into three taxonomic races (*Indica*, *Maxima* and *Moharia*). Principal coordinate analysis was performed on 12 qualitative traits for each of the biological races, separately that resulted in the formation of 29 clusters. From each cluster, 10% of the accessions were selected to constitute a core collection of 155 accessions. The composition and diversity of the core collection was validated by the χ^2 -tests of the frequencies of origin, races, subraces and data on qualitative traits. The analysis of the quantitative traits for mean, range, variance, Shannon-Weaver diversity index and phenotypic associations indicated that the diversity from the entire collection was optimally represented in the core collection (ICRISAT, 2023).

Breeding Objective: The major breeding objectives of foxtail millet are developing high-yielding cultivars which produce protein-rich seed and are resistant to diseases, pests, and lodging, and are adapted to local ecological conditions (Hermuth *et al.*, 2016).

Breeding method: In foxtail millet, pureline selection was the most widely adopted breeding method for improving grain yield in the initial period. Single plant selections were made from landraces and improved varieties and the superior progenies were tested in multilocations and promising progenies were identified as variety (Ganapathy *et al.*, 2021). Recombination breeding has not been exploited to the extent done in sorghum and pearl millet mainly due to autogamous nature of crop, small size florets and difficulties in hybridization. Very low degree of natural cross-pollination was observed in foxtail millet. Sufficient high parent heterosis is expressed in foxtail millet for grain yield and on the basis of average heterosis the F_1 s generated about 60%–70% greater average yield compared to parents. Although high significant heterotic effects were observed, additive effects were exploited widely. Significant correlations between traits of estimates of additive effects and/or variety heterosis effects led to understanding that some genes

affecting grain yield, plant height and spike length were either the same of coupling phase linkage. Identification of experimental hybrids by contact method resulted in low frequency of true hybrids. Some of the early efforts in genetic improvement of foxtail millet resulted in the identification of varieties as early as 1940s (Ganapathy *et al.*, 2021). For exploitation of heterosis, male sterile lines were developed in China such as dominant and recessive genetic male sterile lines and photosensitive nuclear line, gene interaction male sterility lines, cytoplasmic male sterility and cytoplasmic genetic male sterility. Despite the development of several male sterile lines, partial genetic male sterile line (PAGMS) is used successfully in hybrid production. Exploitation of heterosis through use of genetic male sterile lines has been major factor for increased foxtail yields in China. Zhangzagu5, a high yielding hybrid has yielded up to 12 t/ha compared to 4.5–6 t/ha in conventional cultivars. However, most of the present developed male sterility used sources as Chang 10A, whose cytoplasm was contributed by Qinyuanmujizui (Ganapathy *et al.*, 2021).

Breeding: Foxtail millet breeding is mainly carried out in China and India. Major breeding objectives are developing high-yielding cultivars which produce protein-rich seed and are resistant to diseases, pests and lodging, and adapted to local ecological circumstances. In China, for example, cultivars with a short growing cycle and a high drought and cold tolerance have been developed; these can be grown in the summer season after winter wheat. The recommended cultivar in Kenya is 'KAT/FOX-1'; it matures in 3–4 months. Techniques applied in foxtail millet breeding include selection, hybridization (using male-sterile lines) and radiation-induced mutations. Due to the floral morphology (very small flowers) and flowering behaviour of foxtail millet, artificial cross-pollination is difficult, but an effective procedure for artificial hybridization of foxtail millet has been developed in the United States. High levels of heterosis for grain yield (67%) and panicle length (68%) have been found (Brink, 2006). One of the important components of plant breeding programmes has been crop improvement through the introduction of novel genes from wild relatives with the research focused on salt stress responses in foxtail millet seedlings. In the Czech Republic, the breeding of foxtail millet accessions is performed by the Gene Bank of the CRI. The collection of foxtail millet includes 42 accessions in an active collection and 150 genotypes in a working collection. The main aim is to find foxtail millet genotypes as a new source of gluten-free grain, a source of feed for animals (hay and seeds) as well as for biomass production used in power plants. Based on the work with genetic resources of foxtail millet, a broad set of foxtail genotypes were chosen which were further selected. The main sources of new genotypes are other gene banks, universities, or botanical gardens all over the world. Because some foxtail millet genotypes may be sensitive to daylight duration, the sensitivity to the day length is the main parameter of the evaluation. During the vegetation, several morpho-phenological characteristics and health assessment of plants were done. After harvest, all genotypes unsuitable for the temperate conditions of the Czech Republic were excluded from the collection. The evaluation was focused on the early-ripening genotypes, on the size of grains, as well as on production of high amount of biomass described by the plant height. In 2014, a new perspective variety of *Setaria italica* 'Ruberit' was bred in the Czech Republic suitable for the production of biomass, human consumption (corn), and livestock nutrition (grain and forage). New genotype of *Setaria italica* 'Rucereus' bred for conditions of the Central Europe (Hermuth *et al.*, 2016).

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 (Hariprasanna *et al.*, 2017). Although there is a long history of foxtail millet cultivation in China, modern foxtail millet breeding was only initiated in China in the 1950s and 1960s, with significant progress being made since the 1980s. Most of the research on foxtail millet breeding has been conducted in China, where it is an important regional cereal. The main research activities from the 1950s to 1970s were comparisons among landraces and individual selection, followed by cross-based pedigree selection in the 1970s. These comparisons and cross-based pedigree selections contributed greatly to foxtail millet improvement in China, including the development of the super cultivars 'Yugu 1' and 'Zhaogu 1' in the 1980s. Radiation and chemical-induced mutations have also been used in foxtail millet breeding to create novel types, such as dwarf lines. Although different types of male sterile lines have been developed over the past 50 years in China, only partial genetic male sterile lines (PAGMS) have been used successfully in hybrid seed production, allowing the use of heterosis to become a reality in recent years (Diao and Jia, 2017). There are currently only two foxtail millet core collections, in China and India. Large-scale screenings of trait-specific lines have been conducted mainly in China, and have identified some special landraces, including those that are resistant to drought. There are many publications describing the inheritance of foxtail millet morphological characteristics in China, with the important ones being reviewed in this chapter. Dominant qualitative traits, including seedling, leaf sheath, and anther color, have been used as markers to identify hybrids. The estimated heritabilities of quantitative characteristics, such as plant height, panicle length, and heading date, have been useful for foxtail millet breeding programs. Additionally, the recent detection of significant quantitative trait loci has helped to characterize the underlying genetic mechanisms regulating specific traits. Cytological studies of foxtail millet are summarized in this chapter, especially those involving the trisomic Yugu 1 cultivar (Diao and Jia, 2017).

moisture and heat stress and its mechanisms is discussed. The improvement of yield potential, climate resilient traits together with nutritional superiority can make millets as future climate smart crops (Ganapathy *et al.*, 2021). Realizing the importance of small millets and lack of organized research efforts, the Indian Council of Agricultural Research established the All India Coordinated Small Millets Improvement Project in 1986 with its headquarters in University of Agricultural Sciences, Bangalore. Since then, concerted efforts in germplasm collection, recombination breeding and crop production and protection have resulted in development and release of many improved cultivars for commercial cultivation by the dryland farmers along with improved package of practices. Development of early maturing, high yielding and drought-resistant varieties with emphasis on both grain and biomass continue as important breeding objectives in all the small millets. Breeding methodologies aiming at recombination breeding slowly started gaining momentum in all the small millets though the progress is hampered by typical floral biology and anthesis behaviour. In the last three decades, more than 200 improved cultivars have been released by adopting different breeding approaches to suit the location-specific requirements of the farmers. This chapter describes the breeding efforts made in different small millets crops and progress so far in India in other countries (Tonapi *et al.*, 2022).

Interspecific hybrids: An interspecific cross between foxtail millet (*Setaria italica*) and wild relative *Setaria viridis* as undertaken in order to introduce from the latter Triazine resistance in the cultivated plant. Four backcross generations obtained with *Setaria italica* as recurrent parent were studied. Results show that only two backcross generations associated with selection are enough to eliminate weedy characters and to return to the cultivated types. *Setaria viridis* could thus be an interesting source for improvement of foxtail millet without a complex and time consuming breeding strategy (Naciri *et al.*, 1992).

Table 1. Improved varieties of Foxtail millet or Navane in India

Variety	Year of release	Maturity (days)	Av. yield (q/ha)	Area of adaptation	Special features
Renadu (SiA3223)	2020	86-90	30-35	Andhra Pradesh	High yielding, medium bold grains, tolerant to blast and downy mildew
Garuda (SiA 3222)	2020	60-62	15-18	Andhra Pradesh	Extra early variety
ATL-1 (TNSI 331)	2020	80-85	21-22	Tamil Nadu	Non-shattering, non-lodging, drought tolerant
Hagari Navane-46	2019	85-90	16-18	Zone -1, 2 and 3 of Karnataka	Bigger seed size and medium duration
DHFT 109-3	2018	86-88	28-29	Agro-climatic Zone-3 & 8 of Karnataka	Suitable for contingency planting
Survanandi (SiA 3088)	2018	70-75	20-25	Andhra Pradesh	High seed yield, resistant to blast and downy mildew
RAU-2 (Rajendra Kauni 1)	2017	80-83	23-25	Irrigated and Rainfed upland of Bihar	Resistant to leaf blast, rust, smut, brown spot, downy mildew and leaf blight, high iron and zinc content
SiA 3156	2014	85-90	20-25	All states	High seed yield, tolerant to shootfly
SiA 3085	2011	75-82	20-30	All states	High yielding, resistant to blast and downy mildew
HMT 100-1	2008	90-95	20-25	Karnataka	High tillering, stay green character

Table 2. Foxtail millet varieties in India (Roy, 2021)

State	Popular Varieties in the State
Andhra Pradesh	SiA 3088, SiA 3156, SiA 3085, SiA 326, Lepakshi, Narasimharaya, Krishnadevaraya, PS 4
Karnataka	DHFT-109-3, HMT 100-1, SiA 3088, SiA 3156, SiA 3085, PS 4, SiA326, Narasimharaya
Tamil Nadu	TNAU 43, TNAU-186, Co (Te) 7, Co 1, Co 2, Co 4, Co 5, K2, K3, SiA 3088, SiA 3156, SiA 3085, PS 4
Telangana	SiA 3088, SiA 3156, SiA 3085, SiA 326, Lepakshi
Rajasthan	Prathap Kangani 1 (SR 51), SR 1, SR 11, SR 16, SiA 3085, SiA 3156
Uttarakhand	PS 4, PRK 1, Sreelaxmi, SiA 326, SiA 3156, SiA 3085
Uttar Pradesh	PRK 1, PS 4, SiA 3085, SiA 3156, Sreelaxmi, Narasimharaya, S-114, SiA 326
Bihar	RAU-1, SiA 3088, SiA 3156, SiA 3085, PS 4

Breeding of sorghum and pearl millet has led to quantum jump in productivity especially due to the availability of hybrids in these millets. Breeding of finger millets and other small millets has not received much attention and moreover recombination breeding has not been exploited fully mainly because of the autogamous nature of the reproduction, small sized florets and difficulty in hybridization. This chapter focuses on the genetic resources available and utilization of the available genetic resources for genetic improvement. The inbuilt potential of millets to overcome the vagaries of climate especially

Biotechnology: Its two species, *Setaria italica* (domesticated) and *Setaria viridis* (wild progenitor), have characteristics that classify them as excellent model systems to examine several aspects of architectural, evolutionary, and physiological importance in Panicoid grasses especially the biofuel crops such as switchgrass and napiergrass. Foxtail millet is a staple crop used extensively for food and fodder in parts of Asia and Africa. In its long history of cultivation, it has been adapted to arid and semi-arid areas of Asia, North Africa, South and North America. Foxtail millet has one of the

largest collections of cultivated as well as wild-type germplasm rich with phenotypic variations and hence provides prospects for association mapping and allele-mining of elite and novel variants to be incorporated in crop improvement programs. Most of the foxtail millet accessions can be primarily abiotic stress tolerant particularly to drought and salinity, and therefore exploiting these agronomic traits can enhance its efficacy in marker-aided breeding as well as in genetic engineering for abiotic stress tolerance. In addition, the release of draft genome sequence of foxtail millet would be useful to the researchers worldwide in not only discerning the molecular basis of biomass production in biofuel crops and the methods to improve it, but also for the introgression of beneficial agronomically important characteristics in foxtail millet as well as in related Panicoid bioenergy grasses (Lata *et al.*, 2013).

Varieties: Varieties like Co1, Co2, Co3 were released in 1943. In India, till 2015, about 32 varieties have been released. The short duration varieties like SiA3085, SiA3088 and SiA 3156 are popular among cultivated types in India and have the potential to yield up to 2500 kg/ha (Ganapathy *et al.*, 2021). The improved varieties of Foxtail millet or Navane in India are given in Table 1-2.

USES

The husked grain of foxtail millet is used as food in Asia, south-eastern Europe and Africa. It is most important in China and India. The grain may be cooked and eaten like rice, either entire or broken. It can be ground and made into unleavened bread or, when mixed with wheat flour, into leavened bread. The flour is also made into cakes, porridges and puddings. In northern China foxtail millet forms part of the staple diet; it is usually mixed with pulses and cooked, or the flour is mixed with that of other cereals in the preparation of bread and noodles. It is considered a nutritious food and is often recommended for the elderly and for pregnant women. Since the 1990s it has been used in China for the industrial preparation of mini crisp chips, millet crisp rolls and flour for baby foods. Foxtail millet is used in the preparation of beer and alcohol, especially in Russia and Myanmar, and for vinegar and wine in China. Sprouted seeds are eaten as a vegetable, *e.g.* in China. In Europe and the United States foxtail millet is primarily grown as bird feed. It is an important fodder crop ('moha'); in the United States and Europe it is grown for hay and silage, and in China the straw is an important fodder. The straw is also used for thatching and bedding, *e.g.* in India. The bran serves as animal feed and can be used for oil extraction. Foxtail millet is credited with diuretic, astringent and emollient properties and is used to treat rheumatism. It can be sown in contour strips for erosion control (Brink, 2006). It is usually cooked whole like rice or made into meal. In addition, foxtail millet is consumed as stiff porridge called sargati, or as leavened bread known as roti, after the de-hulled grain has been milled into flour. Other food applications are pudding, breads, cakes, chips, rolls, noodles, etc. Foxtail millet is fermented to make vinegar and wine in China and to make beer in Russia and Myanmar. Sprouted grains are also eaten as vegetable in some regions (Hariprasanna, 2020).

Traditional uses (SM, 2017)

- The grain of Foxtail millet is used in China as an astringent and emollient in choleric affections and diarrhea.
- The seeds are used in India as a diuretic, to strengthen virility, treat indigestion, dyspepsia and rheumatism.
- It helps to treat food stagnancy.
- The seeds (green) help to reinforce virility.
- The white seeds are useful for fever and cholera.
- In Pakistan, the crushed seeds are combined with ghee and consumed for the sexual vigor or potency.
- The decoction made from *Setaria* oil and bark of *Acacia modesta* is used as a tonic or to raise fertility in females and males.
- It is used in India to enhance vigor and treat bone fractures.
- The cooked grains are used in Chhattisgarh as a cure for diarrhea.

- The paste is externally used as a cure for swellings.
- It is combined with other herbs to cure dysuria.
- In Aurangabad, the decoction made from the whole plant is used internally for rheumatism and reduce the pains caused due to parturition.
- The seeds are used to treat diabetes.
- In Western Himalaya, it is combined with cow's curd in order to treat measles.

Precautions: The sensitive people might get allergic reactions so they should avoid it. It should be consumed in limited amounts.

How to Eat (SM, 2017)

- Seed are consumed as a sweet or savory food.
- Foxtail millet is used as a basic food in North Africa, South and East Asia and South Eastern Europe.
- The grain cooked in milk or water is consumed as rice.
- The seeds are grounded as flour and used to make porridge puddings, cakes and bread.
- The flour made by Foxtail millet is used to make noodles.
- Foxtail millet is combined with pulses in Northern China and cooked.
- In China, it is used to make millet crisp rolls, mini crisp chips and flour.
- In China, it is used to make wines and vinegar.
- In Myanmar and Russia, it is used to prepare alcohol and beer.
- In China, the seeds are sprouted and consumed as vegetable

NUTRITIONAL VALUE

The composition of foxtail millet grain per 100 g edible portion is: water 12 g, energy 1470 kJ (351 kcal), protein 11.2 g, fat 4.0 g, carbohydrate 63.2 g, crude fibre 6.7 g, Ca 31 mg, Fe 2.8 mg, thiamin 0.6 mg, riboflavin 0.1 mg and niacin 3.2 mg. The essential amino-acid composition per 100 g grain is: tryptophan 103 mg, lysine 233 mg, methionine 296 mg, phenylalanine 708 mg, threonine 328 mg, valine 728 mg, leucine 1764 mg and isoleucine 803 mg. The starch granules are spherical, angular or polyhedral with a diameter of 6–17 µm. Most foxtail cultivars are non-glutinous and are thus suitable for the diet of people with coeliac disease. The bran contains about 9% oil (Brink, 2006). Foxtail millet grains are about 2 mm in length and the glumes can be white, red, yellow, brown, or black. Neither white nor red varieties were found to contain tannins. The 1000 kernel weight is about 2.6 g and milling yield is about 77% after removal of the husk and bran. The starch granules in foxtail millet are generally spherical in the floury endosperm, but polygonal forms have also been found. The granule size varies from 0.8 to 9.6 µm. The amylose and amylopectin content of the starch depends on the type of foxtail millet. Foxtail millet can be waxy (high in amylopectin), normal (low amylose) or non-waxy (high amylose). In normal foxtail millet the amylose content can be up to 33%. The protein bodies are mostly spherical and are 1–2 µm in diameter. About 40% of the total extractable nitrogen is prolamin protein and about 20% can only be extracted with a reducing agent. This indicates that foxtail millet, like most other cereals, is rich in prolamin protein but there is a high proportion of disulfide bonds in the protein (Collar, 2008). 100 grams of Foxtail millet contains 12 g of moisture, 351 calories, 11.2 g of protein, 4 g of total fat, 63.2 g of carbohydrate and 6.7 g of crude fiber. It grants 803 g of isoleucine, 1764 g of leucine, 103 g of tryptophan, 328 g of threonine, 233 g of lysine, 0.6 mg of thiamin, 63.2 g of carbohydrate, 2.8 mg of iron, 11.2 mg of protein, 3.2 mg of niacin, 4 g of lipid fat, 0.1 mg of riboflavin and 31 mg of calcium (SM, 2017). Like other millets, foxtail millet is highly nutritious and even superior to rice and wheat in certain constituents. Grains of foxtail millet have low glycaemic index (GI) and high fiber (8%) content. The protein content is higher (12.3%) among millets and major cereals and also the amount of fibers (as β-glucans; 42.6 %). The metabolism of sugar and cholesterol gets increased due to β-glucans resulting in hypoglycemic and hypocholesterolaemic effects, which is beneficial for prevention of diabetes and cardiovascular

diseases. Because of this, foxtail millet is used in the preparation of low GI foods for treating diabetics, particularly type 2 diabetes and also cardiovascular diseases. Clinical trials of foxtail millet diabetic food on diabetic volunteers revealed blood glucose reduction by 14-18%, triglycerides and cholesterol reduction 8-10%, LDL cholesterol reduction by 5% and HDL cholesterol increase by 2-3% (Hariprasanna, 2020). Nutritional Values foxtail millet (Per 100 g) are Protein - 12.3 gm, Fat - 4.3 gm, Minerals - 3.3 gm, Dietary Fibre - 8 gm, Carbohydrates -6.9 gm, Energy - 331 kcal, Calcium -31 mg, Phosphorus -290 mg and Iron -2.8 mg (Origin, 2020).

Foxtail millet like other millets is a powerhouse of nutrition. Rich in Vitamin B12, these tiny seeds can offer you a daily dose of ample protein, good fat, carbs and amazing dietary fibre content. Besides copious amounts of lysine, thiamine, iron and niacin, it also offers copious amounts of calcium (Netmeds, 2021). Foxtail millet is highly nutritious as compared to mainstream cereals. Consuming foxtail millet in diets provides us an overall calorie of 349 Kcal. This millet possesses 30.10 mg/100 g of calcium and 3.73 mg/100 g of iron. Foxtail millet is primarily rich in protein content, followed by a good amount of fat and fiber. The overall protein content in foxtail millet is 11.20 g, and it also has a higher dietary fiber of 4.42 g. Foxtail millet is free of gluten and can be desirably fed to celiac patients. Foxtail millet has a glycemic index ranging from 54 to 68, comparatively lower than the major cereals with a glycemic index greater than 70. Analysis of foxtail millet whole grained flour presented a higher total phenol and total bioactive compounds, revealing a higher radical scavenging activity. The total phenols in the flour are 153 mg/TAE, and it also consists of a higher flavonoid of 173.91 mg/CE/100. Compared to other whole grain flours, foxtail millet had a higher protein digestibility with good quality essential amino acids, polyunsaturated fatty acids, and higher starch digestibility. These features endure foxtail millet as a desirable diet to all age groups (Pramitha *et al.*, 2023). Foxtail millets are packed with the goodness of proteins, carbohydrates, vitamins like Vitamin A and E and minerals like phosphorus, calcium, magnesium, sodium, etc. The nutrients in foxtail millets are mentioned in the Table 3 (Singh, 2023):

Table 3. Nutritional value of foxtail millet

Nutritional components	Value per 100 g
Energy	331 kCal
Protein	12.3 g
Dietary fibre	8 g
Fat	4.3 g
Phosphorus	290 mg
Potassium	250 mg
Magnesium	81 mg
Vitamin A	32 mg
Calcium	31 mg
Vitamin E	31 mg
Folic acid	15 mg
Sodium	4.6 mg
Niacin	3.2 mg
Iron	2.8 mg
Zinc	2.4 mg

HEALTH BENEFITS

Health Benefits (SM, 2017)

Proper function of cardiac: Vitamin B1 assists in the formation of neurotransmitter acetylcholine which helps to transfer the message between muscle and nerves. It also safeguards the functions of cardiac. The deficiency of Vitamin B1 leads to improper functions of cardiac. The patients of congestive heart failure finds Vitamin B1 helpful and prevents heart ailments.

Alzheimer's disease: Vitamin B1 slows the development of Alzheimer's disease. It could be treated with an intake of 100 mg supplements of Vitamin B1. The trial studies are still carried out for the determination of the mechanism due to which it occurs.

Enhance memory: Vitamin B1 helps to enhance the concentration and memory power. It helps to manage the nervous ailments such as Bell's palsy and multiple sclerosis. It is also called morale vitamin which provides a positive impact on nervous system and supports mental perspective.

Antioxidant: Vitamin B1 acts as an antioxidant which slows down the process of age spots, wrinkles and other age related problems that has negative effect on the organs.

Cures muscle weakness: Iron is essential for the maintenance of the health of muscles. It is found in the muscle tissues and transports oxygen which is essential for the muscle contraction. The deficiency of iron leads the muscle to lose the elasticity and tone and may cause anemia.

Brain health: Iron assists in the brain development. It supplies oxygen to the brain, as it uses about 20% of blood oxygen. Iron is directly associated with the brain functions. The adequate amount of blood if received by the brain helps to promote the cognition and prevents Alzheimer's disease and dementia. Due to this the adequate amount of iron is essential for the brain oxygenation.

Restless leg syndrome: The deficiency of iron in the body is the cause for the restless leg syndrome. The low presence of iron in the blood is the cause for this. The high intake of supplements of iron in adequate amounts helps to cure this condition. It is associated with muscle spasms which is the symptoms of deficiency of iron.

Nerve signals: Protein helps in the functions of nervous system smoothly. The activation of nervous system triggers the response of relevant reactions. The receptor sites consist of protein complex which helps to transfer the nerve signals to the cells and manage the central nervous system.

Hair health: Protein is essential for the maintenance of hair health and prevents it from damage. Protein has a vital role in the growth of hairs. Due to the beneficial effects, the hair care products use the protein in it.

Skin health: Proteins support and strengthen the tissues such as skin which is tears constantly. Collagen is considered as the vital protein that strengthens the tissues, cells and organs that is essential for the revitalization. The high presence of collagen protein found in the body provides wrinkle free, healthy and youthful skin. Millets are known as Trinadhanya or Kudhanya in Ayurveda. Ancient Ayurvedic texts like Mahodadhi written by Sushena in the 14th century describe Foxtail millets as sweet and astringent to taste, that increases vata dosha but balances doshas related to pitta, kapha and blood tissues. Millets need to be cooked well for deriving full benefits, however, this particular millet should never be mixed with milk, as it may cause severe indigestion (Netmeds, 2021):

Health Benefits of Foxtail Millet (Netmeds, 2021)

Stronger Bones: Foxtail millets are an excellent source of iron and calcium which play a pivotal role in maintaining the health of bones and muscles. Iron deficiency can cause various health conditions including weaker muscles, anemia, frequent muscle spasms. Include Foxtail millet in your regular diet to meet the calcium and phosphorous needs of the body for combating brittle bones, inflammation and other bone related chronic conditions like osteoporosis, arthritis, spondylitis etc.

Strengthens Nervous System: Nutritionists strongly recommend the intake the Foxtail millet for keeping various neurological disorders at a bay. Loaded with Vitamin B1, this tiny gluten-free cereal gives your 0.59 mg of it, in every cooked 100 grams. Eating this nutritious cereal not only slows down the progression of various neurodegenerative conditions like Alzheimer's, Parkinson's etc but makes a positive impact on the nervous system. The high amount of iron triggers cognitive function by providing more oxygenation to the brain.

Boosts Cardiac Health: Millets are in general popular for maintaining good heart health. Being gluten-free, rich in protein and less on carbs these amazing wonders of nature aid in the formation of neurotransmitter acetylcholine that transfers message between muscle and nerves besides protecting the heart functions. Eat it daily to protect heart from various ailments.

Manages Diabetes: Diabetic patients are generally discouraged to cut down on the intake of rice, owing to its high carb content. Foxtail millet is an absolutely great substitute to rice as it keeps you satiated for longer hours. The trick is to eat thoroughly cooked Foxtail millet in the place of rice for preventing those mid-day hunger pangs and avoid sudden spike in sugar levels. The glycemic index of Foxtail millet is at 50.8 making it an ultimate choice of low-glycemic foods. Include it in daily diet to witness a healthy dip in levels of blood sugars, glycosylated hemoglobin and lipid profile.

Lowers Bad Cholesterol: Foxtail millet contains a good source of amino acids including Lecithin and Methionine which play a crucial level in decreasing cholesterol by reducing excess fat in the liver. The presence of Threonine prevents fatty liver, further decreasing the levels of bad cholesterol.

Triggers Weight Loss: Tryptophan, an amino acid present in Foxtail millet in ample amounts is crucial for preventing hunger pangs. If you are one of those battling excessive fat around the belly, it's time to increase the intake of Foxtail millet as it prevents accumulation of fatty substances in the body.

Promotes Digestion: Happy gut is an indication of overall health. Digestive issues if not addressed early can turn chronic and may lead to severe constipation, diarrhea or irritable bowel syndrome. It is an amazing choice of food for those with gluten intolerance or celiac disease. Eat it with loads of vegetables to regulate bowel movements and to lose weight.

Builds Immunity: In these days and times of pandemic, nothing is more important than a robust immunity. A rich source of vitamins, minerals and other nutrients, Foxtail millet ups the stamina, keeps you stronger and builds immunity for fighting various infections lurking around. If you have fallen ill recently to any of the viral or bacterial infections, include it in daily diet for gaining the strength back. Literature studies state that the occurrence of diabetes can be lowered by including whole grains like foxtail millets in your diet. In vitro study in 2003 concluded foxtail millets have a low glycemic index and may stimulate the cells of pancreas to produce insulin, a hormone which regulates blood glucose. These actions can help lower the spike in blood glucose. Consuming foxtail millet may help manage diabetes. However, more human trials are needed to support the claims obtained from animal experiments and in-vitro studies (Singh, 2023).

Potential uses of foxtail millets on hypertension: Hypertension or high blood pressure is a leading risk factor for many cardiovascular diseases. Hypertension is usually managed with drugs belonging to a class called as "ACE inhibitors", they work by relaxing the blood vessels which helps in reducing the blood pressure. ACE-inhibitor molecules are also found in food sources like foxtail millet. Chen et al. conducted a study in 2017 stating the consumption of foxtail millets caused a reduction in blood pressure in hypertensive rats. This indicates that the consumption of foxtail millet can have a positive impact on blood pressure. However, we need more studies to support these claims.

Potential uses of foxtail millets in colorectal cancer: Colorectal cancer is cancer of the colon and the rectum, located at the lower end of the digestive system. Literature suggests that the intake of whole grains or cereals can contribute to a lower risk of colorectal cancer. A study done by Zhang et al. in 2020 to assess the effects of foxtail millets on colorectal cancer showed that the ingestion of foxtail millet positively impacted colorectal cancer in mice. This suggests that consuming foxtail millets may help manage colorectal cancers. However, we need more clinical studies to support these claims.

Potential uses of foxtail millets for fungal infections: To date, many chemical compounds obtained from plants have positively impacted fungal infections. Foxtail millets may inhibit the growth of these fungi and, thus, show antifungal activity against these species. This indicates that foxtail millets may have the potential to manage fungal infections, but we need more clinical studies to support these claims.

Potential uses of foxtail millets in under nutrition: Under nutrition (insufficient energy and nutrient intake is broadly divided into stunting, underweight, wasting and micronutrient deficiencies. The main cause of under nutrition is a deficiency in nutrient intake. It was conducted that a meta-analysis in 2022, stating that adding millets to the diet may help improve under nutrition due to the presence of nutritional components like methionine (an essential amino acid), calcium, protein, zinc. The findings of this study support the use of foxtail millets as a solution to under nutrition. However, more studies should be conducted in humans to ascertain these claims.

Other potential uses of foxtail millets: Foxtail millets are rich source of iron, which is required for the formation of haemoglobin, thus an increased iron intake may help manage iron-deficiency anaemia. The presence of insoluble fibres in foxtail millets reduces the risk of gallstones by reducing the production of bile acids (end products of cholesterol metabolism) and decreasing bile cholesterol levels. The fibre content in millets aid bowel movements and may provide relief from constipation.

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