

# Foxtail Millet: A Climate-Resilient Crop Species with Potential to Ensure Food and Agriculture Security Amidst Global Climate Change

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## ABSTRACT

Foxtail millet is one among the earliest cultivated and climate-resilient crop species with an immense nutritional profile. They are adapted to grow under a wide range of harsh environmental conditions ranging from high temperature to drought and salinity. It does not demand proper irrigation, artificial soil nutrients or insecticide. But they are incredible with their nutritional contents; almost five to ten times more nutritionally richer than the extensively consumed rice or wheat in terms of micronutrients, fibres and vitamins. It is a staple food crop in the various regions of Asia and Africa. The current COVID-19 pandemic and forthcoming environmental challenges may lead to the instability of agriculture and food security. Therefore, foxtail millet may serve an emissary crop to meet the demand of food supply for humans and cattle as well as rejuvenate other economically important crops against environmental constraints through biotechnological approaches.

**Keywords:** Foxtail millet, food security, agriculture security, model crop, abiotic stress.

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## INTRODUCTION

Global warming, anomalous average rainfall, flood, expanding soil salination and atmospheric waves prevailed at different regions of the globe that resulted in gradual climate change. Both, the natural (solar waves, volcanic eruption, ocean water temperature etc) and artificial (mass deforestation, emission of industrial gases, fossil fuel consumption, increase in greenhouses gases etc.) stress factors have contributed equally to climate change. Rise in atmospheric temperature across the globe is at alarming condition as it is estimated to increase by approximately 4-5°C before the end of 21st Century (Tollefson, 2020). Increase in the level of sea water is another atrocity of climate change which hastens the process of soil salination. Gradual salination of fertile landmasses is posing complications to the affected farmers to produce food at their maximum yield. The maximum areas of agricultural lands that are affected by salinity are in Australia, followed by Central and North Africa, Southern part of America and West and South Asia. Another calamitous consequence of climate change is drought which happens due to low rainfall, declination of ground water level, heat stress and salinity. The effect of occurrence of combination of heat and drought or drought and salinity is more devastating for crop yield than the individual stress when occurs separately (Dreesen *et al.*, 2012; Zandalinas *et al.*, 2018). Up to 70-80% yield loss may occur if severe heat and drought extends throughout the growing season of a particular crop species in a given area (Leng and Hall, 2019). These abiotic stresses impose detrimental impact on agricultural production and weaken global food security.

Foxtail millet [*Setaria italica* (L.) P. Beauv.], is a genetically diverse C<sub>4</sub> photosynthetic panicoid crop with excellent climate change/stress elasticity and nutritional profiles. It is mostly cultivated for food and forage in the arid and semi-arid regions across the globe. Being reared in environments having minimal resources, these crops still retain their potential to withstand

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high temperature, drought, pathogen and pest infection, and poor soil nutrition. In addition, the crop has excellent water- and nitrogen-use efficiency (WUE and NUE) and is phylogenetically adjacent to major cereals and biofuel grasses including napiergrass (*Pennisetum purpureum*), pearl millet (*Pennisetum glaucum*) and switchgrass (*Panicum virgatum*) (Singh *et al.*, 2017). The in-depth genetic and physiological analysis of foxtail millet would reveal the molecular adaptations endured in a naturally abiotic stress tolerant plant. The present article discusses the salient features of foxtail millet along with their nutritional and abiotic stress responsive properties and potential in ensuring global food and agricultural security amidst climate change.

## Genomics and genetic architecture of foxtail millet

Recent advances in the area of plant genomics aided by next generation sequencing (NGS) platforms, advanced molecular biology and biotechnological tools have enabled the extensive study of organism's genome and mining of trait contributing locus even at the level of single nucleotides. Although foxtail millet was one among the earliest domesticated crops, till last decade, it was regarded as an orphan and underutilized crop due to their research negligence and lack of awareness regarding

their high-quality nutritional profile and therapeutic potentials. Considering the socio-economic and agricultural importance of this crop, its genome was sequenced independently by the Beijing Genome Initiative (BGI), China and Joint Genome Institute (JGI) of the Department of Energy, USA to uncover the enigma behind their abiotic stress tolerance potential and admirable nutritive values (Zhang *et al.*, 2012; Bennetzen *et al.*, 2012). Being diploid in nature ( $2n = 2x = 18$ ) with ~415 Mb of size, it comprised the smallest genome among several other millets and related cereals like rice, wheat and maize. The proportion of repeat elements was 46% and composed of different retroelements (31.6%) and transposable elements (9.4%). Altogether, more than 38,000 genes were identified in foxtail millet and mapped against different proteome databases such as SwissProt, KEGG, TrEMBL InterPro and GO for functional annotation. Approximately, 30,579 genes (78.81%) were assigned to biological functions while 8,220 (21.19%) were unannotated. The transcriptome analysis of various tissues and abiotic stress conditions revealed that ~82% of the identified genes are expressive in nature. The comparative mapping of genomes between foxtail millet and other sequenced grass have showed that maximum collinearity with the maize (86.7%) and sorghum (72.1%) genome, followed by rice (71.8) and brachypodium (61.5%) (Muthamilarasan *et al.*, 2017). This indicates the close evolutionary relationship between the genomes of these crops. Phylogenetic analysis of the genus *Setaria* have also revealed that the foxtail millet and sorghum shared a common ancestry around 8.3 million years ago (Vicentini *et al.*, 2008). Later, foxtail millet and its wild ancestor green foxtail (*Setaria viridis*) were separated from maize and sorghum approximately 27 million years ago.

### Foxtail Millet: A C<sub>4</sub> Model Plant for Genomic and Physiological Studies

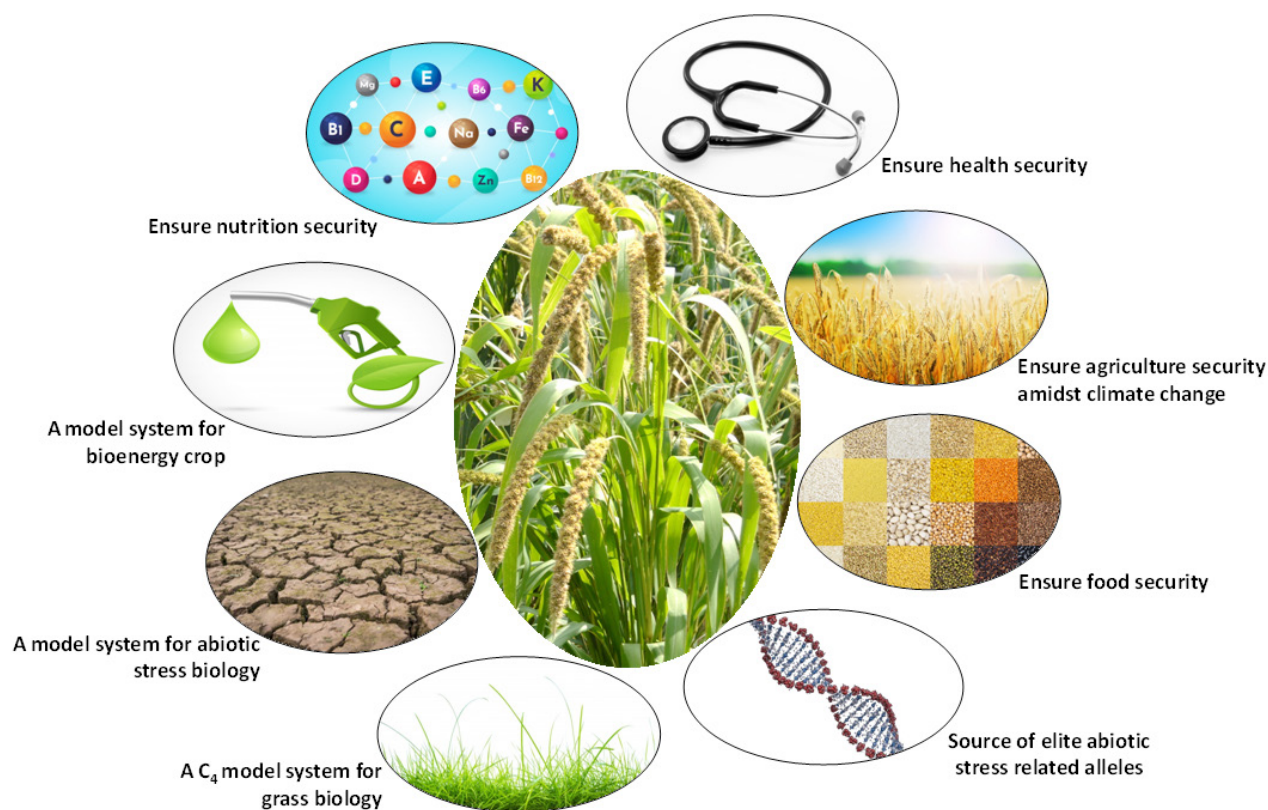
Being a crop of dry land and warm weather with admirable WUE; deep and dense root architecture and reduced leaf area, foxtail millet is well recognized for its resilience against broad-spectrum environmental stresses, especially towards drought and high salt conditions (Lata *et al.*, 2013). It can withstand the challenges posed due to anomalous environmental conditions without compromising the yield. Additionally, short life cycle, inbreeding in nature, lesser genome complexity, availability of genomic resources and genetic relatedness to economically important cereal crops make it an excellent model system to study the molecular mechanism behind environmental stress tolerance and physiology of C<sub>4</sub> photosynthesis. Other than higher photosynthetic efficiency, C<sub>4</sub> photosynthesis provides additional advantages to the plants including superior growth and ecological enactment in warmer conditions, decreased hydraulic conductivity per unit leaf area and improved flexible biomass allocation patterns (Sage and Zhu, 2011). Therefore, C<sub>4</sub> photosynthesis has always been a centre of attraction in cereal science as the important crops such as rice, wheat and barley are C<sub>3</sub> plants, and integration of C<sub>4</sub> traits in these crops will enhance their ecological resilience and productivity. Till date, studies pertaining to C<sub>4</sub> photosynthesis were conducted in maize, sorghum and sugarcane; however, the complexity in their larger genome size along with higher complexity, big stature and prolonged crop cycle were the demerits, which has resulted in inadequate success. Therefore, the need for a C<sub>4</sub>

crop with smaller genome and rapid life cycle is requisite, and foxtail millet is the ideal crop which could serve as a model for studying C<sub>4</sub> photosynthesis.

Foxtail millet confers durable tolerance to multiple abiotic stress including drought, salinity and high temperature (Diao *et al.*, 2014). They do not require irrigation and need around 20-30% of the average rainfall demanded by other crops like rice and banana. Several genetics and genomics studies reported that the foxtail millet contains unique as well as identified abiotic stress-related genes, which attribute in the wide range of abiotic stress adaptation (Singh *et al.*, 2017; Muthamilarasan and Prasad, 2015). Considering foxtail millet as model plant for study biology of abiotic stress, widespread research has been carried out to delineate the roles of a number of abiotic stress-related gene families including AP2/ERF (Lata *et al.*, 2011), DREB (Lata *et al.*, 2014), NAC (Puranik *et al.*, 2013), WD40 (Mishra *et al.*, 2012, 2014), MYB (Muthamilarasan *et al.*, 2014a), C2H2 zinc finger (Muthamilarasan *et al.*, 2014b), WRKY (Muthamilarasan *et al.*, 2015), AGO, DCL, RDR (Yadav *et al.*, 2015), HSPs (Singh *et al.*, 2016), ADP-ribosylation factors (Muthamilarasan *et al.*, 2016a), HSPs (Singh *et al.*, 2016), aquaporins (Singh *et al.*, 2019) and C<sub>4</sub>-photosynthetic pathway associated gene (Muthamilarasan *et al.*, 2020) in abiotic stresses. Recently, a miniature foxtail millet mutant named 'xiaomi' has been developed with Arabidopsis-like life cycle and small architecture (Yang *et al.*, 2020). A single base mutation at the Phytochrome C (*PHYC*) gene was responsible for these features in foxtail millet. This plant will further enhance the acceptability of foxtail millet as a model system for C<sub>4</sub> grass biology and environmental stress related studies (Fig. 1).

### Potential of Foxtail Millet in Ensuring Food and Nutrition Security

Foxtail millet is a perfect example of neglected species that have the potential to address both food and nutritional insecurities prevalent among the ever-growing global population. In terms of any nutritional parameter, it is far ahead of other most popular cereals like wheat and rice. Foxtail millet grains are rich in protein content (12-15%), dietary fiber (6-8%), crude fat (7-8%) and minerals, including iron, calcium and zinc (Muthamilarasan *et al.*, 2016b). Apart from higher protein content, it also contains higher number of essential amino acids and sulfur-containing amino acids, including methionine and cysteine. Foxtail millet has approximately forty times more fibre than rice; dietary fibre is essential for stomach and intestine health. The proportion of resistant starch in foxtail millet flour varies from 13-15%, which is significantly higher than the most commonly consumed cereal grains like rice and wheat. It is an extraordinary beneficial dietary supplement for diabetic patients. In type-II diabetes patients it aids in controlling serum glucose level, reducing serum lipids and glycosylated haemoglobin (Thathola *et al.*, 2010). It is also used for the treatment of dyspepsia, rheumatism, poor digestion and stomach-ache. The other remarkable feature of foxtail millet as food is their low glycaemic index (GI) polysaccharide, gluten free in nature and higher amounts of polyphenols and antioxidant contents. Considering its nutritional prospects, climate-resilient and other aspects, Food and Agriculture Organisation (FAO) of the United Nations has declared the year 2023 as the 'International Year of Millets'.



**Fig. 1:** Foxtail millet serve as an exemplary model system and ensure multiple security including food, nutrition, health and agriculture. Image designed using clip arts available from freepik.com

### Potential of Foxtail Millet in Ensuring Agricultural Security

Foxtail millet contains excellent genetic diversity among the large number of wild as well as cultivated accessions, which are maintained as core and mini core collections around various gene banks across the globe. China encompasses the largest collection of wild and cultivated germplasms of foxtail millet followed by India, France and Japan. These germplasms are the exceptional source of gene pool required for crop improvement programmes. Numerous of these germplasms could be tolerant to various abiotic stresses, mostly to heat, drought and salinity, and their phenotypic and physiological attributes must be exploited for crop improvement through genomic-assisted breeding (GAB) and biotechnological approach. The availability of whole genome sequence has prompted the development of high throughput genomic resources, detection of molecular markers/quantitative trait loci (QTLs), comparative mapping, and GAB of foxtail millet and related grained crops. Transcriptome and whole genome RNA sequencing (RNA-seq) platforms are being utilized to identify large number of abiotic stress related genes; among which some of them are specific to foxtail millet (Zhang *et al.*, 2007; Lata *et al.*, 2010; Qi *et al.*, 2013; Liu *et al.*, 2016; Yu *et al.*, 2020). The integrative omics approach comprising of genomics, transcriptomics, phenomics, metabolomics, proteomics and bioinformatics would provide extensive insight regarding genetic determinants of such stress tolerance attributes in foxtail millet. Miserably no such integrative approach has been attempted in foxtail millet till date, however independent metabolome and proteome analysis

have been carried out to identify stress-responsive determinants (Veeranagamallaiah *et al.*, 2008; Guo *et al.*, 2018; Pan *et al.*, 2018).

The transfer of foxtail millet's genic regions contributing enhanced stress tolerance to the highly cultivated though stress susceptible crops such as rice, wheat or others may resuscitate the agricultural loss due to adverse climatic conditions. For example, the integration of foxtail millet Autophagy-associated gene, *SiATG8a* into the rice genome resulted in the improved tolerance to abiotic stress and nitrogen starvation (Li *et al.*, 2016). Similarly, the overexpression of stress-related transcription factors including *SiMYB3* and *SiWLM2b* have exhibited nitrogen starvation and drought tolerance in rice, respectively (Ge *et al.*, 2019; Yang *et al.*, 2019). Targeted genome editing is another widely accepted technology employed to generate improved crop plants. The application of recently emerged Clustered regularly interspaced short palindrome repeats (CRISPR)/CRISPR-associated protein (Cas) technology has the potential to design climate smart plant species. The DNA sequence of foxtail millet genome may be taken as reference in order to detect polymorphism among the genome of related crops and targeted base editing at stress tolerance providing locus may alter their environmental stress response.

### CONCLUSION AND FUTURE PROSPECTS

The foremost challenge of the present situation is to ensure food and nutrition security for all. Food security would not be possible without ensuring agricultural security. Anomalous climatic conditions are continuously posing threat to optimum crop yield and independent studies from various

organizations alarming that the conditions will become more precarious. Naturally, foxtail millet is rich in minerals, nutrients and bioactive compounds and less dependent on synthetic fertilizers, systemic irrigation and pest/weed control. They serve as an excellent resource material for abiotic stress related gene function dissection and elite allele mining. Therefore, it could be concluded that the foxtail millet has the potential to fulfil the purpose of food and nutrition security in one hand and resuscitate the agriculture system on the other hand. Biotechnological tools have made it possible to design the crop of our desire taking the foxtail millet genome as reference.

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