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Millets in the limelight: wonder crops for combating climate change and nutritional security

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Agriculture is at a great risk on a global scale as because the areas that are most vulnerable to climate change include but are not limited to Africa, Asia and Latin America. As a result, we will witness increase in severe weather events, such as droughts, floods and heat waves which may disrupt crop production systems causing the loss of biodiversity. Consequently, it is important that plants that can survive these unfavorable conditions are found. Millets, small-seeded cereals that make up a group known for its ability to grow under unfavorable conditions including drought stress, stand out as an option revealing promise due to their unique adaptability in marginal environments. Having diverse origins and among the most ancient grains ever known, millets number about 6,000 species globally with rich nutritional composition and genetic diversity; thus they represent a practical choice toward enhancing climate resilience in agriculture through adoption at local levels worldwide. In this paper, we look at the biology of millets. We discuss their uniqueness in terms of domestication history plus their stress tolerance and climate resilience, features that set them apart from other cereal crops. Additionally, we delve into their major nutritional qualities, broad adaptability and genetic potential which all contribute to making millets a standout crop choice. Gene editing and biotechnological approaches take center stage as instrumental in hastening domestication efforts while still engineering high yielding millets that hold onto their climate resilience, a two pronged priority approach for enhanced production on one hand and preserving biodiversity on the other. In light of the changing climate patterns, it is clear that focusing on enhancing and growing millet on a large scale is essential for building resilient agriculture and securing food sources.

Keywords: *agriculture, climate change, genetic diversity, millets, nutrition, resilience*

Introduction

The practise of agriculture, along with the apparent production of commodities for diverse employment, is also about managing a definitive ecosystem, subjective of various turbulences impacted by living and non-living entities, the latter being those we have least control over, yet. The word “climate” is defined as the prevailing conditions of the abiotic factors affecting the farmland including seasonal temperature, rainfall averages, wind patterns *etc*., the long-term alteration of which being notoriously acclaimed as the climate change. Feulner (2017) estimates that global temperatures will increase by 1.6-6.0 °C and average precipitation will rise by over 2% due to climate change by 2050, which in turn results in severe weather conditions, like droughts, floods and heat waves. On a worldwide scale, it is predicted that agriculture will be affected by the expected climatic changes, with Africa, Asia and Latin America being the region most at risk (Ayanlade et al., 2018). There are considerable facts that crop yields (Shortridge, 2019), biodiversity (Bálint et al., 2011) and temporal dynamics of total precipitation are all being significantly affected by the climate change. The content and patterns of the cultivational scenario, as a direct interaction to the environment is also privy to the looming threats of heating up, freezing down, changing behaviours of water and air and therefore requires sustainable adjustments in what to grow in the minimal and how to make most of it. Looking for crops that are hardy and resilient and at the same time, capable of harbouring the essential nutritional potential has led to the revival of millet crops, a group of small-seeded cereals, that had to wait on the side-lines for a long time to finally make it to the limelight on the global food spectrum that had been ruled by regular staples like wheat and rice, since the green revolution during 1960s.

Among the oldest crops for humans were millets and they are considered to be the first cereal that man ever cultivated for domestic consumption. Millet is a term used for several yearly grasses with small seeds belonging to five groups, *viz*., Panicum, Setaria, Echinocloa, Pennisetum and Paspalum of the Paniceae tribe, and Eleusine from Chlorideae tribe. Among the most cultivated varieties include pearl millet, sorghum, finger millet, proso millet (common or hog), foxtail millet (often called 'Italian' in India) and barnyard millet (small isolated spikelets). In both Africa and semi-arid tropics of Asia, where other crops are hard to grow due to harsh climate conditions like droughts *etc*., such as pearl millets have been staple food crops since time immemorial. They have been grown since long ago. Chandrasekara & Shahidi (2010) mentioned that around 6,000 varieties of millet are grown globally. Small millets such as finger millet, foxtail millet, pearl millet, little millet, proso millet, kodo millet, barnyard millet, browntop millet, guinea millet and more are included in this group of millets. They are primarily grown on a small scale in less favorable environments. The rich nutritional profile and genetic diversity of millet grains make them potentially capable of causing the next green revolution, as acknowledged by Goron & Raizada (2015). Millets are increasing in importance in marginal environments that are particularly at risk to changes in climate, like increased temperatures and erratic rainfall, with long-term global warming potential (Padulosi et al., 2009). Millets may be a suitable option for farming in areas such as India and West Africa, which face difficulties due to low precipitation and sandy, slightly acidic soil conditions (Changmei & Dorothy, 2014). Millets are important grains that can help prevent food scarcity and famine by being able to grow well in dry conditions (Amadou et al., 2013). In this article, we explore the fundamental biology and special evolution process of millets, emphasizing characteristics that enhance their ability to withstand stress and adapt to climate changes in comparison to other top cereal crops. We focus on key nutritional qualities, broad adaptability and genetic potential of millets and their potential for revealing characteristics. We highlight the benefits of using gene editing and biotechnology to accelerate the domestication and improve the resilience of productive millets in response to changing climates. In conclusion, we suggest that promoting and growing millets on a large scale could be crucial for fostering climate resilient agriculture.

Millet as a promising alternative cereal

Many of the morpho-physiological, molecular and biochemical characteristics possessed by the millets which offer better resilience to environmental stresses are absent in the major cereals. The short life cycle amounting to 12-14 weeks (seed to seed) of these coarse grains fundamentally assists in stress whereas rice and wheat are more yielding to the abiotic pressures with a long growth phase of about 20-24 weeks. Nevertheless, several useful traits like short stature, less leaf area, thickened cell walls, dense rooting *etc*. aids in evading the extent of stress conditions and their repercussions (Li & Brutnell, 2011). Moreover, possessing the C_4 photosynthetic characteristic is extremely beneficial for millets. The C_4 pathway enhances the CO_2 concentration in the bundle sheath cells, essentially suppressing the photorespiratory activity (upto 80%) with respect to the temperature levels and elevates the interior catalytic activity of the enzyme RuBisCO (Sage et al., 2011). Due to the elevated CO_2 levels in C_4 crops, millets exhibit significant rates of photosynthesis even in warm conditions, and demonstrate nitrogen-use efficiency and water-use efficiency that are approximately 1.5 to 4 times higher than plants using the C_3 mechanism (Sage et al., 2011). For example, foxtail millet needs 257 g of water per gram of dry gram, while wheat and maize needs 510 g and 470 g, respectively (Li & Brutnell, 2011; Bandyopadhyay et al., 2017). C_4 photosynthesis not only improves water and nitrogen use, but also offers advantages such as increased growth and ecological performance in hot weather, improved distribution of biomass and reduced hydraulic conductivity per unit leaf area (Sage et al., 2011; Bandyopadhyay et al., 2017). Millets possess these characteristics that position them as crops of the future, offering research opportunities to explore desirable traits like climate resilience and apply the findings to improve key cereal crops. Efforts have been made to engineer C_4 traits in rice by studying millets as a model, but it is essential to recognize the stress tolerance potential of millets to further advance the development of climate-resilient crops.

Stress tolerant genetic systems

Millets' remarkable capability to endure different abiotic stresses such as drought, salinity, light, and heat makes them an ideal subject for studying their reactions to stress on cellular, molecular, and physiological levels (Bandyopadhyay et al., 2017). Numerous millet stress adaptation strategies have been identified in studies exploring their morphology, physiology and biochemistry. For instance, Bidinger et al. (2007) noted that the flowering timing of pearl millet is controlled by the rainfall patterns. Balsamo et al. (2006) found that teff grass had higher leaf tensile strength in drought conditions; whereas, Ajithkumar & Panneerselvam (2014) noted an increase in root length in little millet. In the same way, foxtail millet (Lata et al., 2011), little millet (Ajithkumar & Panneerselvam, 2014) and teff (Smirnoff & Colombe, 1988) have shown an increase in biochemical processes like higher levels of antioxidants, reactive oxygen species, catalase, superoxide enzymatic activities, osmolytes production and stress-related proteins, as a response to environmental stress. van der Weerd et al. (2001) examined the membrane permeability of water in pearl millet and maize in order to achieve ideal water status during osmotic stress conditions. In addition, new genes, alleles, and QTLs have been discovered in millets, and studying their functions has shown how they help improve stress tolerance (Bandyopadhyay et al., 2017). Information on the determinants of climate resilience at a genetic level to be described through association mapping and biparental mapping has yielded limited results till now. Conducting extensive phenotypic screening is essential to discover natural genetic variations in stress tolerance in various millet varieties. This is crucial to fully utilize the inherent genetic potential through traditional and modern breeding methods, as well as cutting-edge genomic and transgenomic technologies. The looming threat of prevailing salinity and drought conditions with scanty rainfall patterns in both millet and non-millet crops cultivations could hugely benefit from the increased focus on basic and applied research in millets to avail and incorporate the sturdiness and resilience of this game changer crop, also leading to enhanced and popularised cultivation of the same, around the world. Let’s look into the unique characteristics of each type of millets that contribute to their resistance to climate change.

1. **Sorghum** (*Sorghum bicolor*)

Despite being a naturally heat-tolerant crop, Sorghum experiences heat stress during key growth stages, which reduces yield. It lowers photosynthetic rate during the vegetative stage and affects pollen viability and fertilization during the reproductive stage (Djanaguiraman et al., 2018). Impa et al. (2019) stated that terminal water stress in sorghum led to a reduction in individual grain size and diameter and an increase in grain hardness. The decrease in grain-filling duration during drought conditions causes the grain-filling process to finish sooner, resulting in smaller grain size and reduced number of grains (Impa et al., 2019). Pang et al. (2018) and Chadalavada et al. (2021) also observed decreased test weight, grain size and grain hardness in sorghum when subjected to low soil moisture conditions. Drought stress decreases a number of enzyme activities involved in starch production and accumulation, depending on the severity of drought stress (Pang et al., 2018), lowering the grain's overall starch content. However, numerous studies found that during drought stress, grain protein content increased (Sarshad et al., 2021), while protein digestibility decreased one of the crucial elements affecting the calibre of sorghum feed (Chadalavada et al., 2021). However, other investigations found that irrigated sorghum grain samples had enhanced kernel hardness and protein content (Njuguna et al., 2018). Protein content is inversely correlated with starch content, according to Wu et al. (2011), a finding that has a detrimental impact on the biofuel sector by lowering the amount of ethanol that can be produced from sorghum grain samples. We could use the underutilised gene pool to create significant climate-resistant sorghum cultivars if we understood the wild ancestors of sorghum. A major problem lies in the genetic barriers that prevent wild relatives' genes from being introduced into domesticated sorghum species. However, more genomic data are now available thanks to the recent development of next-generation sequencing (NGS), which broadens and extends the sorghum improvement programmes employing the novel, as of yet unexplored genes in sorghum's wild relatives (Ananda et al., 2020; Chaturvedi et al., 2022). Sorghum germplasm's temperature sensitivity and photoperiod are crucial determinants for locating reliable sources for creating cultivars with a wide range of adaptation, as well as photoperiod and temperature insensitive germplasm. The tall accessions that are highly sensitive to light periods can be utilized to enhance biomass and fodder, making this breeding approach well-suited for both India and the USA (Upadhyaya et al., 2021). Chen et al. (2017) utilized GWAS to distinguish heat tolerance genes in sorghum during the vegetative phase. Twenty-five heat shock transcription factors for sorghum were identified in another genome-wide research (Nagaraju et al., 2015) that revealed how the plant responded to various abiotic stresses. Elevated temperature stress led to the expression of Hsf1 (heat stress transcription factors), while drought stress led to the expression of Hsf5, 6, 10, 13, 19, 23 and 25. These genes shed light on abiotic stress-tolerance mechanisms under various conditions. Research by Johnson et al. (2014) on sorghum's response to drought and heat stress stated that 4% of genes were found to have different expression levels under drought conditions, while 17% showed altered expression under heat stress. Furthermore, a discovery was made of 7% of distinct genes related to the combined stress response. Identifying the genes that are expressed differently could potentially enhance sorghum's ability to withstand heat and drought in varying climate conditions.

2. **Pearl millet** (*Pennisetum glaucum*)

Pearl millet is able to survive in severe weather conditions and low-quality soil and can still yield a significant amount of grain; in contrast, other cereals like rice, wheat, maize, sorghum and barley may struggle to thrive (Satyavathi et al., 2021). It offers various forms of security such as food, livelihood, health and ecological benefits, distinguishing it as a crop of agricultural security, unlike wheat and rice which mainly focus on food production. Due to its ability to tolerate high temperatures, thrive in dry regions and be grown in certain parts of India, this crop is considered resilient to climate change effects (Gupta et al., 2015). In India, the progression of pearl millet breeding has advanced from open-pollinated cultivars to single cross hybrid development through extensive collaboration between CGIAR and NARS institutes. To ensure lasting genetic advantages, it is essential to combine hybrid parent lines in a heterotic group to speed up hybrid breeding for regions in South Asia and Sub-Saharan Africa that are susceptible to drought. To improve pearl millet breeding, researchers have developed and used diverse molecular markers as well as genomic tools that help in identifying QTLs/genes, determining genetic diversity and implementing Marker Assisted Breeding (MAB). For instance, among other molecular markers identified for pearl millet are RFLP (Liu et al., 1994), RAPD, AFLP (Devos et al., 1995), STSs (Allouis et al., 2001), SSRs (Meena et al., 2020) and SNPs (Sehgal et al., 2012). Nowadays several genetic markers and genomic techniques provide a comprehensive insight into plant biology thereby supporting Marker-Assisted Breeding (MAB) for the production of new resilient hybrids and varieties. Proteomics technology allows determination of post-translational modifications, protein concentrations, protein-protein interactions, structures associated with stress tolerance as well as regulatory activities of gene-encoded proteins (Satyavathi et al., 2021). Understanding stress-regulated pathways can be improved by identifying and studying stress-responsive genes and proteins in pearl millet. Moreover, it may be employed to develop techniques for improving the stress tolerance as well as resistance levels of other similar crops like pearl millet. Several proteome studies exist on this cereal crop; therefore further research could explore C_4 photosynthesis in detail (Ghatak et al., 2021; Weckwerth et al., 2020). As a result of transcript expression profiling, two markers sensitive to high temperatures, Pgcp70 and PgHSF, were discovered for categorizing a gene from the sHSP group in pearl millet under high-temperature stress conditions (Chaturvedi et al., 2022). Screening physio-biochemical traits of different genotypes of pearl millet inbred lines at the seedling stage helped identify PgHSP20 genes, enhancing knowledge of molecular control in stress tolerance (Chaturvedi et al., 2022) and potential strategies for coping with abiotic stress unpredictability (Satyavathi et al., 2020).

3. Foxtail millet (*Setaria italica*)

Foxtail millet is a beneficial model system for research exercise, due to its physiological, genetic and climate resilience characteristics (Peng & Zhang, 2021). Setaria, a model C_4 plant with a compact genome, has been the focus of several genetic studies. Foxtail millet was the initial millet employed in genome editing studies, henceforth. Lin et al. (2018) conducted the initial CRISPR/Cas9 genome editing study in foxtail millet. Scientists utilized protoplasts from various monocot and dicot plants, such as foxtail millet, to assess genome editing in individual cells using CRISPR/Cas9. Recently, genome editing using CRISPR/Cas9 was performed to create double haploid (DH) lines in *S. italica* by targeting the SiMTL gene (Cheng et al., 2021). Foxtail millet is seen as a tough plant. To study how each indigenous variety adapts to diverse environments, 312 samples were subjected to thorough resequencing. During this extensive genetic study, a total of 3.02 million SNPs were identified and the identification of SiPRR37 as a regulator of heading date was made. The discovery of the gene that confers resistance to severe conditions in north-eastern ecoregions was made possible by the insertion of a Tc1-Mariner transposon into the first intron (Li et al., 2021). The new findings in foxtail millet germplasms have sparked an interest in sequencing new cultivars to study distinctive characteristics that may be altered through breeding. Niu et al. (2018) found that *Pseudomonas fluorescens*, *Pseudomonas migulae* and *Enterobacter hormaechei*, which are types of plant growth-promoting rhizobacteria (PGPR), were linked to the drought resistance of foxtail millet. In the upcoming years, a mix of OMICS-based techniques could be employed to pinpoint the key factors that affect stress tolerance in foxtail millet, with a focus on drought stress. The knowledge gained from this information will assist researchers throughout the world better understand the mechanisms underlying plants' stress responses and apply it to the development of stress tolerance in other cereal crops.

4. Proso millet (*Panicum miliaceum* L.)

In addition to being an essential part of ATP, the body’s main energy source, the mineral phosphorus present in proso millet aids in the mineral matrix formation that makes up bones (Devi et al., 2014). Roughly 24% of the body’s daily phosphorus requirements can be found in one cup of cooked proso millet. Additionally, phosphorus is a crucial component of nucleic acids that form the basic structure of the genetic code (Kumari & Sumathi, 2002). It is a fast-growing or emergency plant that needs minimal water, rarely faces challenges, is disease-resistant and thrives in various soil and climate conditions.

5. Barnyard millet (*Echinochloa frumentacea* L.)

Because barnyard millet can withstand both biotic and abiotic stresses with little difficulty, it is a rapidly growing crop that can thrive in tough environmental conditions (Renganathan et al., 2020). The grains are highly esteemed for their extraordinary nutritional content relative affordability when compared to other major cereals and additional agricultural benefits. It contains high levels of protein, carbohydrates and fiber, as well as the minerals zinc (Zn) and iron (Fe) (Saleh et al., 2013; Chandel et al., 2014). In a study, Ugare et al. (2014) found that consuming more barnyard millet meal decreased the glycemic index (GI) of those with type 2 diabetes. The data provided indicated that barnyard millets protein content which ranged from 11.2% to 12.7% was marginally higher than that of other notable cereals and millets. Barnyard millet contains up to 18% more iron (mg/ 100 g) than other millets and main grains (Renganathan et al., 2017;

Vanniarajan et al., 2018). Moreover, eliminating hulls in the process has resulted in a notable reduction in phytic acids and a lower phytate level in grains, improving mineral absorption (Panwar et al., 2016). It is widely recognized for its effective nitrogen use in comparison to cereal crops and has been proposed as a natural remedy for removing heavy metals like lead, chromium and cadmium from polluted soils due to its high accumulation capabilities.

6. Kodo millet (*Paspalum scorbiculatum* L.)

Kodo millet is considered as the coarsest cereal of the world. It is found to possess greatest drought resistance of all small millets and has a life cycle lasting 90 to 140 days. It can produce 450-900 kg ha^{-1} and is a resilient plant that can survive dry conditions and prosper in infertile land where other plants may fail (Heuzé et al., 2012). Kodo millet is grown in agricultural environments that frequently experience the uncertainties of nature, like inconsistent rainfall, lack of moisture and high temperatures, so it is essential for cultivars to have drought resistance in order to sustain production levels (Hariprasanna, 2017).

7. Little millet (*Panicum sumatrense* L.)

Little millet (samai), one of the several millets, is a prominent dryland crop cultivated on a small scale as a poor man's crop that can endure water-logging as well as drought (Kamatar et al., 2013). The crop is sown when the first early rains arrive in the region, which is unsuitable for growing other dry land crops like peanuts, sorghum or ragi because of its exceptionally drought tolerant (Patel et al., 2018). Apart from those mentioned above, there are many millet species which are localised in different corners of the world, harnessing valuable genetic potential, but are seldom studied and stayed obscure from the research world. Brown top millet, Guinea millet etc. are some examples of these, deserving proper exploration and programmes to be developed into commercialised cultivars.

Collection, documentation and characterization of germplasm

Various institutions worldwide have access to over 28,041 unique finger millet germplasms. The International Crop Research Institute for the Semi-Arid Tropics (ICRISAT) holds 5,957 germplasms and the National Bureau of Plant Genetic Resources (NBPGR) has 10,507 germplasm. For the advancement of all crop species, genetic and genomic resources are very crucial, where genetic resources drive breeding progress and genomic resources aid in the thorough analysis of genetic resources for identifying valuable genes, alleles and QTLs to enhance crops. Millets possess abundant genetic resources, but they have less information on genomic resources like molecular markers and physical/genetic maps compared to major cereals (Goron & Raizada, 2015; Bandyopadhyay et al., 2017). The ability to access foxtail millet's genome sequence information has enabled the development of different high-throughput genome-wide molecular markers (Zhang et al., 2014; Yadav et al., 2015; Bandyopadhyay et al., 2017) and integrated marker databases (Muthamilarasan & Prasad, 2015; Bandyopadhyay et al., 2017). Many extensive genotyping studies, including examining genetic variation, producing detailed physical and genetic maps and pinpointing QTLs linked to dietary traits, will undeniably depend on these resources.

Genomics-assisted breeding in agricultural improvement has attracted recent attention because it combines traditional and molecular breeding techniques for crop enhancement. Because genome sequence data is accessible, Foxtail millet has a higher potential for creating genomic resources for genomics-assisted breeding when compared to other millets varieties. Furthermore, the utilization of advanced genome sequencing technology has made it possible to create high-throughput molecular markers in different types of millet crops (Bandyopadhyay et al., 2017). After sequencing the transcriptomes of high and low seed calcium genotypes in finger millet, hundreds of microsatellite markers containing SSRs were identified (Kumar et al., 2015). The utilization of genome-wide data along with high-throughput techniques like genotyping by sequencing (GBS) and genome-wide association mapping studies (GWAS) helps in discovering new genes/alleles or QTLs responsible for nutritional characteristics (Varshney et al., 2014; Bandyopadhyay et al., 2017). Two finger millet genotypes, ML365 and PR202, have now their genomes sequenced and made accessible to researchers. Through allele discovery, DNA marker development, genetic mapping and candidate gene identification for drought tolerance and other agronomically significant qualities, finger millet output will increase in the upcoming days, as a result of these genome sequencing efforts (Mahesh et al., 2022). According to Varshney et al. (2017), the Tift 23D2B1-P1-P5 genotype is estimated to have 38,579 genes in its 1.79 Gb draft whole genome sequence. They draw attention to the substantial density for wax production genes, which may help explain why this crop is more tolerant to heat and drought. By resequencing and analysing 994 pearl millet lines, Varshney et al. (2017) were able to get understanding on domestication, genetic diversity and population structure.

The millet scenario of india - current challenges and the way forward

In the previous times, millets were grown and consumed in large quantities in the nation, covering almost as much land as both rice and wheat. Despite having a variety of uses and advantages, nutria-cereal cultivation drastically decreased in the post-green revolution era, falling by 41.65% between 1950-51 and 2018-19 (Sukumaran et al., 2022). In the modern diet, millets are significant as an upgraded of important nutrients, particularly in developing and underdeveloped nations (Anbukkani et al., 2017). Even though millets have a wide variety and excellent nutritional content, their consumption, particularly by the Indian population, has not increased significantly because of a number of reasons. The start-up revolution to increase access to nutrient-rich food and generate employment has recently been slowly fuelled by these grains (Sukumaran et al., 2022).

Conclusion

Millets are acknowledged to hold promising potential for food security and nutrition in the perspective of increasing agricultural expenses, climate change and a growing global population. Millets are sometimes referred to as "orphan cereals" because of their frequently low yield and related agronomic issues; nevertheless, this is merely a matter of viewpoint. Millet's resilience qualities come from its exclusive evolutionary background, domestication in semi-arid regions and continuous selection for stability instead of high yields. Due to the intricate genetic foundation of tolerance to abiotic stress, it will be difficult to reproduce millets' extensive resilience in traditional cereals. Rather, attention should be directed towards improving the yield characteristics of millets and transitioning global production towards these important underutilized crops. They require much lower input expenditures for production are naturally resilient to the majority of biotic and abiotic stressors and have extra health benefits. These characteristics highlight millets as the preferred crop for the global populace notwithstanding rising concerns about climate change. Due to these factors, there is an increasing necessity to study the natural genetic diversity found in their varied collections of genetic resources of plant to enhance crops in terms of various important agricultural and nutritional characteristics. Discovering genes, alleles and QTLs that control traits in crops using NGS technologies and high-throughput GWAS platforms allows for the quicker and enables more precise creation of breeding lines for enhancing crops. Furthermore, as millets share a common ancestry in the poaceae family and have significant alignment of genomes, it is important to focus on them again for the advancement of cereals and bioenergy grasses.

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