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Genomic and biochemical insights into millet adaptation: A pathway to climate-resilient agriculture

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Abstract
Millets, a group of resilient crops, are gaining recognition as key players in sustainable agriculture, particularly in the context of climate change. These crops possess remarkable stress tolerance capabilities, enabling them to thrive under harsh environmental conditions such as heat, drought, salinity, and low light levels. Unlike traditional cereals like rice and wheat, millets can flourish in environments that are challenging for other crops, owing to their unique biological characteristics. These include a short growing season, an efficient C4 photosynthetic pathway, and robust, deep-rooted systems that enable them to conserve water and withstand extreme temperatures. Advancements in both genomic and biochemical research have significantly improved our understanding of the mechanisms underlying millet's resilience to stress. From a genomic perspective, several key genes associated with drought tolerance, oxidative stress resistance, and salinity adaptation have been identified.. However, it is the biochemical changes that millets undergo during stress that are particularly noteworthy. The accumulation of osmo protectants such as proline, soluble sugars, and other stress-responsive metabolites helps mitigate the damage caused by dehydration and oxidative stress. Additionally, the activation of antioxidant defense systems plays a crucial role in protecting millet plants from oxidative damage and maintaining cellular integrity during environmental stress. These biochemical adaptations, along with the genetic factors identified through genomic research, collectively enhance millet's ability to survive and maintain productivity under challenging conditions. This review explores the importance of both genomic advancements and biochemical changes in improving millet stress tolerance. The integration of genomic resources with traditional breeding methods, combined with a deeper understanding of millet's biochemical responses to stress, offers promising avenues for developing more resilient millet cultivars. By leveraging these insights, we can better prepare millets as a cornerstone of climate-resilient agriculture, helping to secure food production in a world increasingly impacted by climate change.

Keywords: Millets, genetics, biochemical changes, foxtail millets

Introduction
Millets are a group of hardy, drought-resistant crops that have gained significant attention for their potential to contribute to sustainable agriculture, particularly in the face of climate change. These resilient crops are well-suited to thrive in environments that are too harsh for many other cereals, including rice and wheat. One of the most notable features of millets is their short growing period, typically ranging from 3 to 4 months, allowing them to escape the peak periods of environmental stress that longer-growing crops, such as rice and wheat, endure, which typically require 5 to 6 months. This ability to avoid prolonged exposure to adverse conditions gives millets a distinct advantage in regions prone to erratic weather patterns or water scarcity [1].

Millets possess a variety of physiological and morphological characteristics that help them withstand extreme environmental conditions. Their relatively short stature, small leaf size, and thickened cell walls enable them to minimize water loss and reduce the surface area exposed to the elements. Moreover, their deep and robust root systems allow them to access water from deeper soil layers, enhancing drought tolerance. These traits, coupled with their efficiency in nitrogen and water usage, make millets highly adaptable to challenging growing environments.

At the biochemical level, millets benefit from the C4 photosynthetic pathway, which is a key factor in their stress tolerance. This unique photosynthetic process allows millets to utilize carbon dioxide more efficiently by reducing photorespiration, a process that competes with photosynthesis and can reduce plant growth, particularly under hot and dry conditions. The C4 pathway not only enhances the efficiency of carbon fixation but also improves the crop's overall growth and heat tolerance. This is particularly advantageous in environments with high temperatures, where C3 plants like rice and wheat may experience reduced productivity due to increased photorespiration [2].

In addition to the C4 photosynthesis pathway, millets have a remarkable ability to grow and thrive with significantly less water than other major cereals such as maize and wheat. Their water use efficiency is superior, allowing them to survive in regions with limited water availability. This makes millets an ideal crop for regions prone to droughts or irregular rainfall, which are becoming more common due to climate change. The ability of millets to maintain efficient growth, biomass distribution, and heat tolerance further underscores their potential as a valuable crop for developing climate-resilient agricultural systems.

Table 1: Genes Involved in Stress Tolerance

Millet	Gene	Nature of study
Foxtail millet	Argonaute protein 1 encoding gene	AGO1b has been shown to regulate stress response in
		foxtail millet
	Abscisic acid stress ripening gene (ASR)	Overexpression of ASR1 in tobacco confers tolerance to
		drought and oxidative stress
	Autophagy-related gene (ATG)	Overexpression of ATG8a in *Arabidopsis* confers
		tolerance to nitrogen starvation and drought stress
	Late embryogenesis abundant protein (LEA)	Overexpression of LEA14 in *Arabidopsis* and foxtail millet
		confers tolerance to salt, osmotic and drought stress
	ABA-responsive DRE-binding protein (ARDP)	Overexpression of ARDP in *Arabidopsis* and foxtail millet
		confers tolerance to salt and drought stress
	WD-40	Identification of the association of WD40 in dehydration
		stress-responsive pathway
	Acetyl-CoA carboxylase	Overexpression of Acetyl-CoA carboxylase in maize
		confers resistance to sethoxydim herbicide
	Dehydration-responsive element-binding protein	Cloning and characterization of DREB2 showed its role
	2 (DREB2)	in conferring dehydration tolerance
	NAC transcription factor	Cloning and characterization of NAC078 showed its role
		in conferring salinity tolerance
	Si69	Overexpression of wheat aluminum induced protein
		(Wali) domain containing protein in *Arabidopsis* confers
		aluminum tolerance
	Aldose reductase	Identification of the association of respective genes in
		salinity stress-responsive pathway
	Glutamine synthetase	
	Pyrroline-5-carboxylate reductase	
	12-oxophytodienoic acid reductase (OPR1)	Cloning and characterization of OPR1 showed
		hormone-independent role of OPR1 in conferring
		drought tolerance
	Photosystem II D1protein	Identification of the association of Photosystem II D1protein-encoding gene in conferring atrazine resistance
	Phospholipid hydroperoxide glutathione	Cloning and characterization of PHGPX showed its
	peroxidase (PHGPX)	association in conferring salinity tolerance
Finger millet	Phosphate transporters (Pt)	Cloning and characterization of four Pt genes which
		showed their involvement in Pi stress
	NAC transcription factor	Overexpression of NAC67 gene in rice confers tolerance
		to salinity and drought stress
		Overexpression of NAC1 gene in tobacco confers
		tolerance to different abiotic stresses
	bHLH transcription factor	Overexpression of bHLH57 gene in tobacco confers
		tolerance to salinity, oxidative and drought stress
	Dehydrin7	Overexpression of Dehydrin7 gene in tobacco confers
		tolerance to drought stress
Pearl millet	Glutathione reductase	Identification and characterization of genes and their
		families highlighted their putative involvement in
		stress-responsive pathways
	Dehydroascorbate reductase	
	Late embryogenesis abundant protein (LEA)	
	β-carbonic anhydrase	
	Ascorbate peroxidase	
	Heat shock factor	
	Voltage-dependent anion channel (VDAC)	Structural and functional characterization of VDAC along
		with heterologous over-expression in yeast which
		showed tolerance to several abiotic stresses

Overall, the combination of their unique physiological traits and efficient biochemical processes, such as C4 photosynthesis, enables millets to survive and even flourish in environments where other crops might fail. These characteristics position millets as a promising candidate for addressing the challenges posed by climate change, offering a sustainable solution for ensuring food security in a rapidly changing world. As climate conditions become more unpredictable, the cultivation of millets holds great promise for creating agricultural systems that are both resilient and resource-efficient, supporting the need for crops that can withstand the rigors of a warming planet. These traits make millets a valuable crop for developing climate-resilient plants [1, 2].

Millets: Model for Experiment to Stress Tolerance

Drought, heat, salinity, and light, such type of stress can be easily handled by millets, making them as an example of great model to examine what are plants responds to these type of stresses. There are so many results about millets adaptability towards stress in different ways. For instance, Pearl millet changes its flowering time based on rainfall [3]. and that little millet grows longer roots under stress [4]. Specific changes in biochemical aspects like higher antioxidants levels and stress-related proteins, have also been recorded in foxtail millet [5] and teff [6]. Additionally, several genes governing stress tolerance have been discovered in millets (Table 1) [7].

Foxtail Millet: An Absolute Model for Stress Tolerance

The millet whose study has been done widely is Foxtail millet as compared to other millets, with help of so many genetic engineering tools and techniques developed for it particularly [8]. From the whole genome sequencing, it has been recorded that it contains 1,517 genes from which 586 genes are related to water response only and these help the plant survived dry and drought conditions. Several studies also recognised important genes for the C4 photosynthesis process, with foxtail millet having more genes for malate dehydrogenase (7 genes) and pyruvate orthophosphate dikinase (3 genes) than other crops. From phylogenetic analysis it has been reported that the expression of Ft_CA1 gene is highl in the mesophyll and that can be important for analysing the Foxtail millet C4 pathway [9].

Fig 1: Different types of Fox tail millets showing different types of grains

However, the understanding is not clear at molecular level for stress tolerance in millets. There is a need of further research to unfold the factors at genetic level for stress resistance, and screening different millet cultivars can help to explore the complete potential. This will lead to develop more resilient crops through breeding and genetic tools and technologies, which is important to enhance crop's response against climate change.

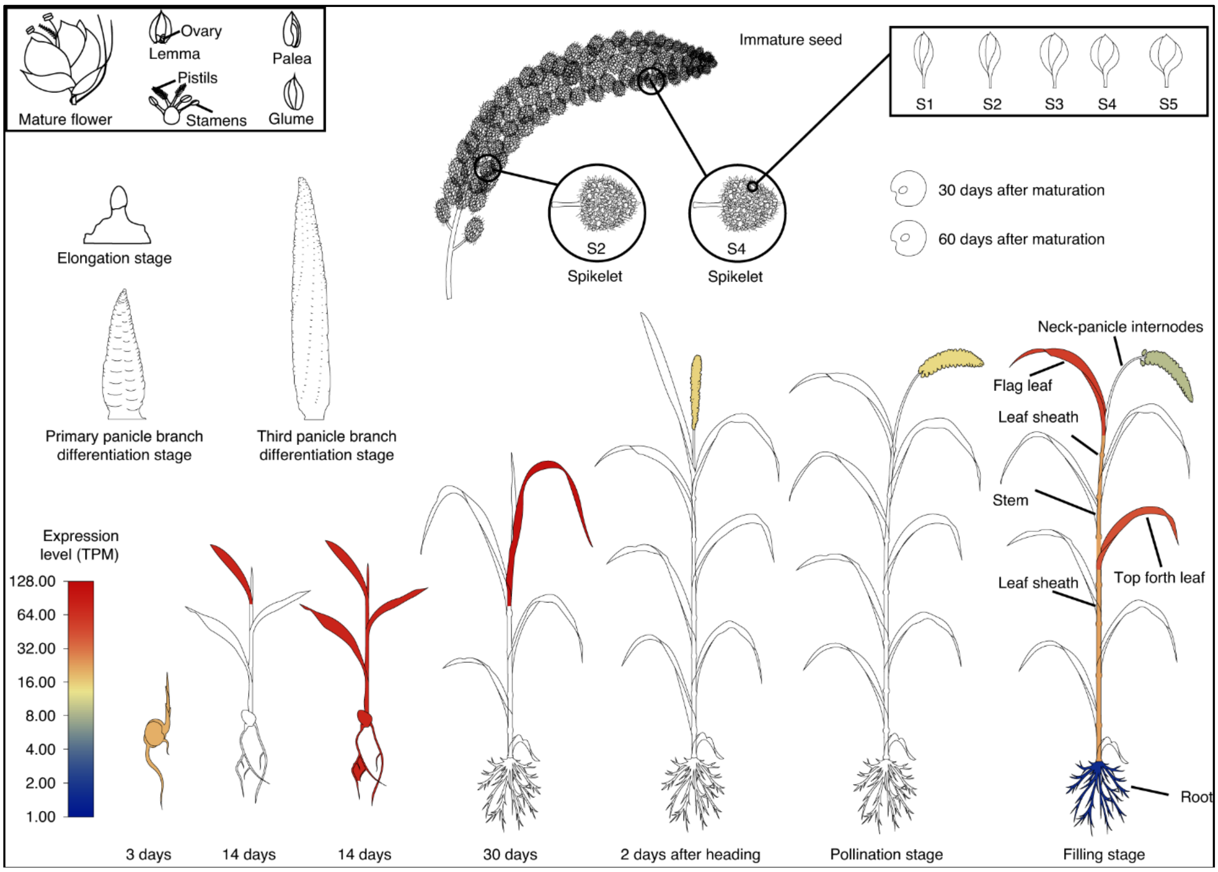

Fig 2: Mini foxtail millet as a new C4 model species (Nat. Plants)

Genomic Resources in Millets

The knowlwdge of genetic and genomic resources are essential for crop improvement. While genomic resources provide great insights to identify useful genes, alleles, and Quantitative Trait Locis for enhancing crop enhancement but for the breeding purpose genetic resources have major role. There are abundant genetic resources present in millets but genomic resources are limited [10, 11]. These genomic resources includes molecular markers and genetic maps are more abundant in major cereals. Integrated marker database and different molecular markers having high throughput have been developed from the genome sequence of foxtail millet [12-18]. So for the study about large-scale genotyping, resources like genetic diversity analysis and nutritional trait mapping QTLs are the key. These tools have been used in 200 foxtail millet and identified microsatellite markers linked to agronomic traits specifically yield traits, which contributes up to 25% of phenotypic variation. These markers will help in uplifting agronomic as well as nutritional characters in millets [19]

Genome-assisted breeding has received a velocity in the direction improvement of crops combining next-generation sequencing with traditional and molecular breeding tools techniques. The gene sequence of Foxtail millet makes a perfect match for Genome-assisted breeding, from which other millets are also getting benifits. Thousands of SSR markers also recorded from the transcript to some analysis of finger millet particularly analysing low and high calcium genotypes [20]. Similarly, SSR markers have been developed for tef [21]. Genome sequencing of pearl millet and finger millet is also ongoing, further expanding genomic resources for crop improvement.

Biochemical changes in finger millet [*Eleusine coracana* (L.) Gaertn.] under drought stress

Biochemical changes Occur in Millets due to stress

An increase in proline content was observed under drought stress compared to the controls in all genotypes of millets. This increase in proline accumulation was more pronounced in drought-sensitive varieties than in drought-tolerant varieties [22]. While proline accumulation has been widely studied in relation to drought stress, its exact role in drought tolerance remains unclear. Some studies have suggested that proline accumulation is a universal symptom of leaf dehydration, indicating stress susceptibility, while others have found that drought-tolerant varieties tend to accumulate more proline than sensitive ones. Despite the variations, the present study suggested that proline may not be a reliable indicator of drought tolerance in the selected genotypes. Additionally, drought stress resulted in an increase in water-soluble carbohydrates (WSCs), particularly sucrose, in the leaves of all genotypes [23]. Sucrose accumulation was significantly higher in sensitive varieties, and the levels varied according to the growth stage and genotype. Other soluble sugars, such as glucose and fructose, were also elevated, likely due to a decrease in respiration rates and the downregulation of glycolysis during drought stress. These sugars, along with raffinose and stachyose, are linked to drought stress tolerance mechanisms, potentially playing a role in mitigating oxidative damage [24].

Drought-induced oxidative stress was reflected by the increased accumulation of malondialdehyde (MDA) in the leaves, a marker of lipid peroxidation. The extent of MDA accumulation was higher in sensitive varieties compared to the drought-tolerant varieties, indicating greater membrane damage in the sensitive varieties under stress. The activities of antioxidant enzymes, including superoxide dismutase (SOD), catalase (CAT), and guaiacol peroxidase (GPX), were elevated under drought conditions, indicating an active defense mechanism against oxidative stress [25]. However, genotype-specific variations in the enzyme activities were observed, with SOD activity being higher in sensitive varieties at certain stages, while CAT activity was higher in tolerant varieties. Different biochemical changes has been shown in Fig 3, 4 & 5 [26].

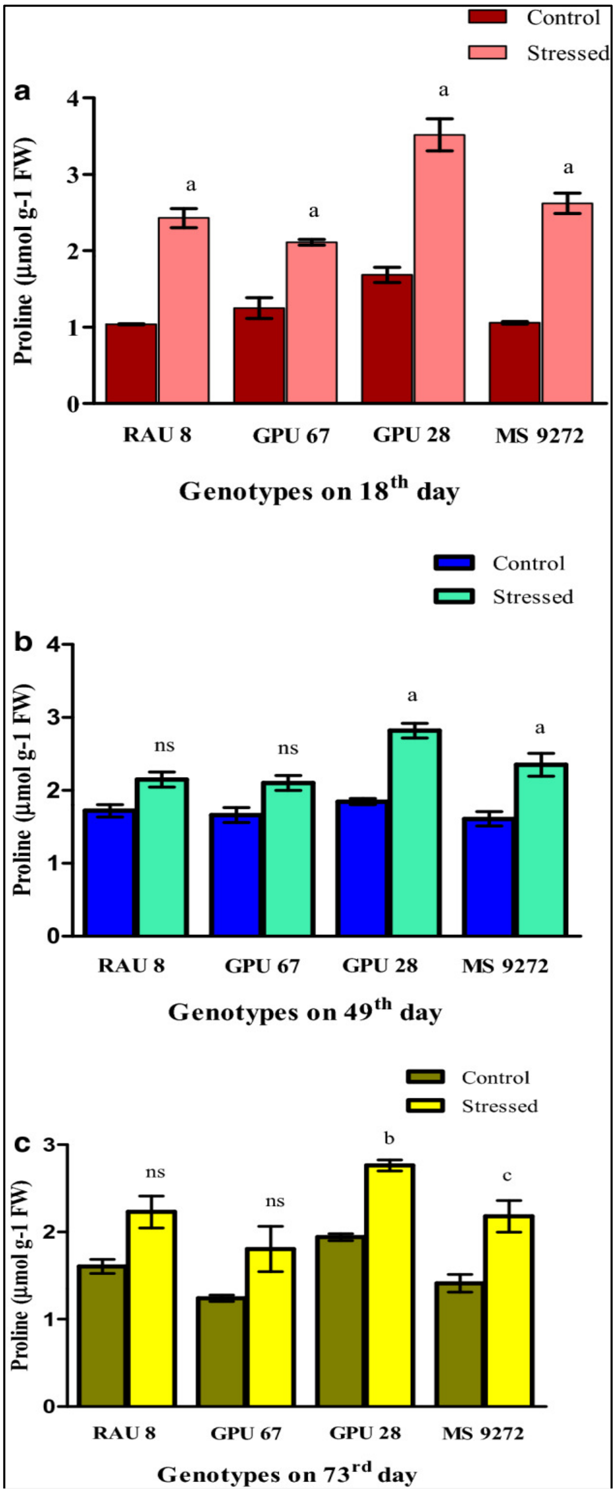

Fig 3: Changes in proline content in four finger millet genotypes during control and drought stress on 18th (**a**), 49th, (**b**) and 73rd DAS (**c**).

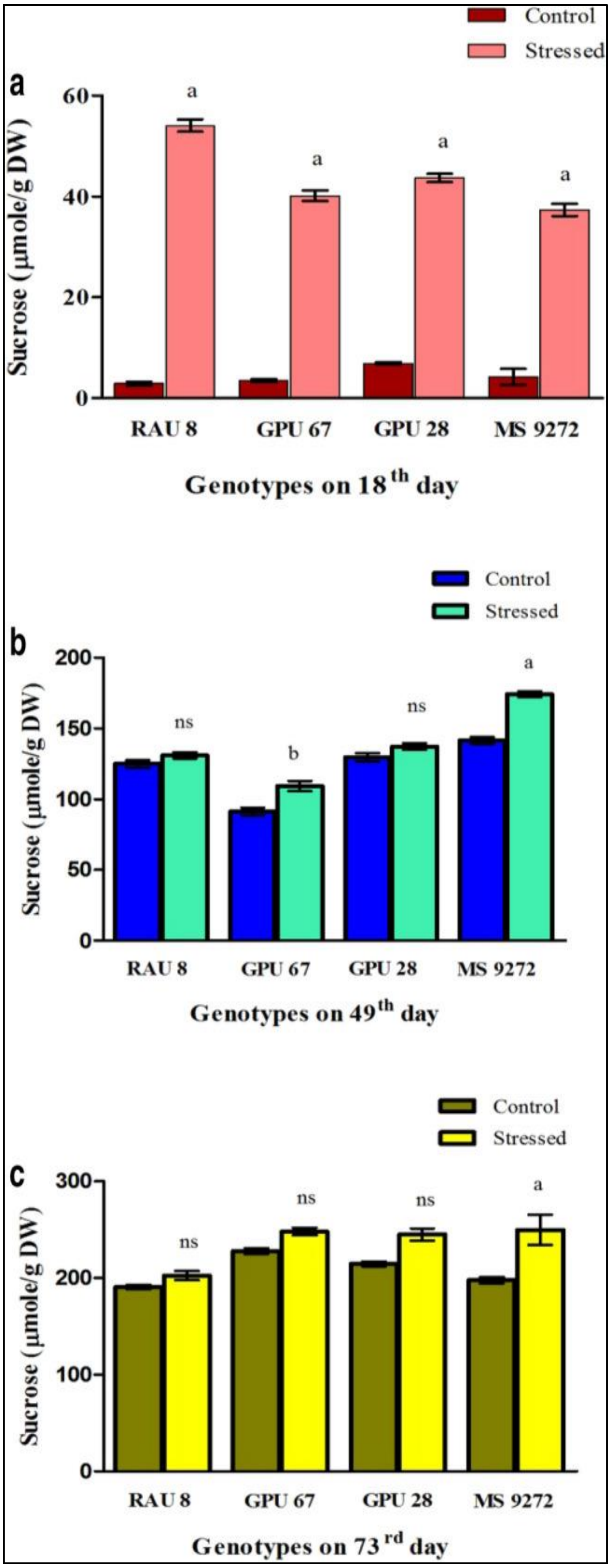

Fig 4: Changes in sucrose content in four finger millet genotypes during control and drought stress on 18th (a), 49th (b) and 73rd DAS (c).

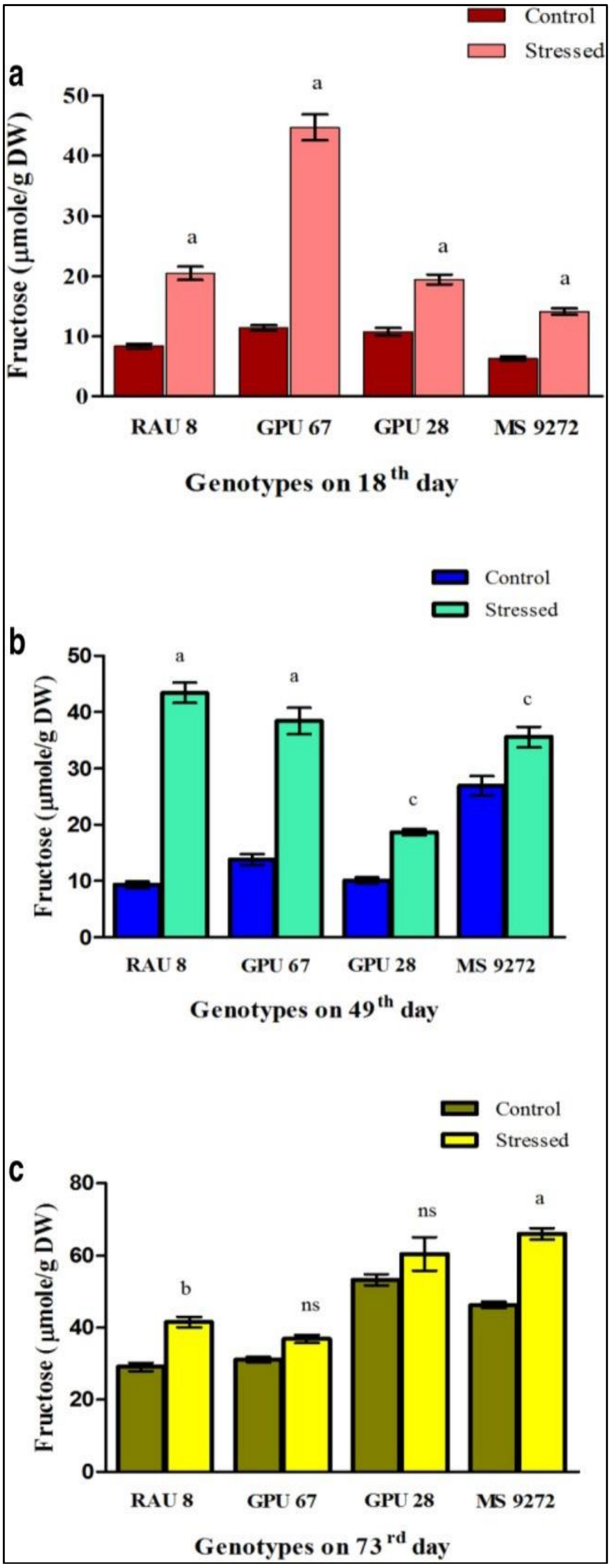

Fig 5: Changes in fructose content in four finger millet genotypes during control and drought stress on 18th (a), 49th (b) and 73rd DAS (c)

Conclusion

Millets have great potential to improve food security and nutrition, especially with rising agricultural costs, climate change, and a growing global population. They are nutritious, provide extra health benefits, need fewer resources to grow, and are naturally resistant to many stresses. These qualities make millets an ideal choice as we face climate challenges. To make the most of millets, we need to study the genetic differences in their varieties and work on improving important traits like yield and nutrition. New technologies like next-generation sequencing (NGS) and genome-wide association studies (GWAS) make it faster and easier to find genes linked to these traits, helping to develop better crops. The growing focus on millets also benefits other crops, like cereals and bioenergy grasses, since they share a common genetic background and have similar genomes.

References

1. Li P, Brutnell TP. *Setaria viridis* and *Setaria italica*, model genetic systems for the Panicoid grasses. J Exp Bot [Internet]. 2011 Mar 31;62(9):3031-3037. Available from: http://dx.doi.org/10.1093/jxb/err096
2. Sage RF, Zhu XG. Exploiting the engine of C4 photosynthesis. J Exp Bot [Internet]. 2011 May 1;62(9):2989-3000. Available from: http://dx.doi.org/10.1093/jxb/err179
3. Bidinger FR, Nepolean T, Hash CT, Yadav RS, Howarth CJ. Quantitative trait loci for grain yield in pearl millet under variable postflowering moisture conditions. Crop Sci [Internet]. 2007 May;47(3):969-980. Available from: http://dx.doi.org/10.2135/cropsci2006.07.0465
4. Ajithkumar IP, Panneerselvam R. ROS scavenging system, osmotic maintenance, pigment and growth status of *Panicum sumatrense* Roth. under drought stress. Cell Biochem Biophys [Internet]. 2013 Sep 26;68(3):587-595. Available from: http://dx.doi.org/10.1007/s12013-013-9746-x
5. Lata C, Bhutty S, Bahadur RP, Majee M, Prasad M. Association of an SNP in a novel DREB2-like gene *SiDREB2* with stress tolerance in foxtail millet (*Setaria italica* L.). J Exp Bot [Internet]. 2011 Mar 17;62(10):3387-3401. Available from: http://dx.doi.org/10.1093/jxb/err016
6. Smirnoff N, Colombé SV. Drought influences the activity of enzymes of the chloroplast hydrogen peroxide scavenging system. J Exp Bot [Internet]. 1988;39(8):1097-1108. Available from: http://dx.doi.org/10.1093/jxb/39.8.1097
7. Bandyopadhyay T, Muthamilarasan M, Prasad M. Millets for next generation climate-smart agriculture. Front Plant Sci [Internet]. 2017 Jul 18;8:1266. Available from: http://dx.doi.org/10.3389/fpls.2017.01266
8. Muthamilarasan M, Dhaka A, Yadav R, Prasad M. Exploration of millet models for developing nutrient-rich graminaceous crops. Plant Sci [Internet]. 2016 Jan;242:89-97. Available from: http://dx.doi.org/10.1016/j.plantsci.2015.08.023
9. Zhang S, Tang C, Zhao Q, Li J, Yang L, Qie L, et al. Development of highly polymorphic simple sequence repeat markers using genome-wide microsatellite variant analysis in foxtail millet (*Setaria italica* L. P. Beauv.). BMC Genomics [Internet]. 2014 Jan 28;15(1):78. Available from: http://dx.doi.org/10.1186/1471-2164-15-78
10. Goron TL, Raizada MN. Genetic diversity and genomic resources available for the small millet crops to accelerate a new green revolution. Front Plant Sci [Internet]. 2015 Mar 24;6:157. Available from: http://dx.doi.org/10.3389/fpls.2015.00157
11. Saha D, Gowda MVC, Arya L, Verma M, Bansal KC. Genetic and genomic resources of small millets. Crit Rev Plant Sci [Internet]. 2016 Jan 2;35(1):56-79. Available from: http://dx.doi.org/10.1080/07352689.2016.1147907
12. Jia X, Yuan J, Shi Y, Song Y, Wang G, Wang T, et al. A Ser-Gly substitution in plastid-encoded photosystem II D1 protein is responsible for atrazine resistance in foxtail millet (*Setaria italica*). Plant Growth Regul [Internet]. 2007 Apr 24;52(1):81-89. Available from: http://dx.doi.org/10.1007/s10725-007-9181-3
13. Kumari K, Muthamilarasan M, Misra G, Gupta S, Subramanian A, Parida SK, et al. Development of eSSR-markers in *Setaria italica* and their applicability in studying genetic diversity, cross-transferability and comparative mapping in millet and non-millet species. PLoS ONE [Internet]. 2013 Jun 21;8(6):e67742. Available from: http://dx.doi.org/10.1371/journal.pone.0067742
14. Pandey P, Achary VMM, Kalasamudramu V, Mahanty S, Reddy GM, Reddy MK. Molecular and biochemical characterization of dehydroascorbate reductase from a stress-adapted C4 plant, pearl millet (*Pennisetum glaucum* L. R. Br). Plant Cell Rep [Internet]. 2013 Dec 8;33(3):435-445. Available from: http://dx.doi.org/10.1007/s00299-013-1544-9
15. Muthamilarasan M, Prasad M. Advances in *Setaria* genomics for genetic improvement of cereals and bioenergy grasses. Theor Appl Genet [Internet]. 2014 Sep 20;128(1):1-14. Available from: http://dx.doi.org/10.1007/s00122-014-2399-3
16. Yadav CB, Muthamilarasan M, Pandey G, Khan Y, Prasad M. Development of novel microRNA-based genetic markers in foxtail millet for genotyping applications in related grass species. Mol Breed [Internet]. 2014 Jun 26;34(4):2219-2224. Available from: http://dx.doi.org/10.1007/s11032-014-0137-9
17. Zhang G, Liu X, Quan Z, Cheng S, Xu X, Pan S, et al. Genome sequence of foxtail millet (*Setaria italica*) provides insights into grass evolution and biofuel potential. Nat Biotechnol [Internet]. 2012 May 13;30(6):549-554. Available from: http://dx.doi.org/10.1038/nbt.2195
18. Muthamilarasan M, Venkata Suresh B, Pandey G, Kumari K, Parida SK, Prasad M. Development of 5123 intron-length polymorphic markers for large-scale genotyping applications in foxtail millet. DNA Res [Internet]. 2013 Oct 1;21(1):41-52. Available from: http://dx.doi.org/10.1093/dnares/dst039
19. Gupta S, Kumari K, Muthamilarasan M, Parida SK, Prasad M. Population structure and association mapping of yield contributing agronomic traits in foxtail millet. Plant Cell Rep [Internet]. 2014 Jan 12;33(6):881-893. Available from: http://dx.doi.org/10.1007/s00299-014-1564-0

20. Kumar A, Gaur VS, Goel A, Gupta AK. De novo assembly and characterization of developing spikes transcriptome of finger millet (*Eleusine coracana*): a minor crop having nutraceutical properties. Plant Mol Biol Rep [Internet]. 2014 Sep 26;33(4):905-922. Available from: http://dx.doi.org/10.1007/s11105-014-0802-5
21. Cannarozzi G, Plaza-Wüthrich S, Esfeld K, Larti S, Wilson YS, Girma D, et al. Genome and transcriptome sequencing identifies breeding targets in the orphan crop tef (*Eragrostis tef*). BMC Genomics [Internet]. 2014 Jul 9;15(1):581. Available from: http://dx.doi.org/10.1186/1471-2164-15-581
22. Bates LS, Waldren RP, Teare ID. Rapid determination of free proline for water-stress studies. Plant Soil [Internet]. 1973 Aug;39(1):205-207. Available from: http://dx.doi.org/10.1007/bf00018060
23. Oufir M, Legay S, Nicot N, Van Moer K, Hoffmann L, Renaut J, et al. Gene expression in potato during cold exposure: Changes in carbohydrate and polyamine metabolisms. Plant Sci [Internet]. 2008 Dec;175(6):839-852. Available from: http://dx.doi.org/10.1016/j.plantsci.2008.08.010
24. Heath RL, Packer L. Reprint of: Photoperoxidation in isolated chloroplasts I. Kinetics and stoichiometry of fatty acid peroxidation. Arch Biochem Biophys [Internet]. 2022 Sep;726:109248. Available from: http://dx.doi.org/10.1016/j.abb.2022.109248
25. Elstner EF, Heupel A. Inhibition of nitrite formation from hydroxylammonium chloride: A simple assay for superoxide dismutase. Anal Biochem [Internet]. 1976 Feb;70(2):616-620. Available from: http://dx.doi.org/10.1016/0003-2697(76)90488-7
26. Mude LN, Mondam M, Gujjula V, Jinka S, Pinjari OB, Yellodu Adi Reddy N, et al. Morpho-physiological and biochemical changes in finger millet (*Eleusine coracana* L.) under drought stress. Physiol Mol Biol Plants [Internet]. 2020 Nov;26(11):2151-2171. Available from: http://dx.doi.org/10.1007/s12298-020-00909-9