Journal of Applied Biology & Biotechnology 2026. Article in Press
Available online at http://www.jabonline.in
DOI: 10.7324/JABB.2026.273153

Biotechnology of millets: Current scenario and future prospects (under agricultural biotechnology for climate-resilient crops)

Aditi Kothari Chhajer[1], Vinod Singh Gour[2], Prasann Kumar[3], Amit Raj[3], Pamil Tayal[1], Dhruv Rathi[4], Mohd Sahil[4], S. L. Kothari[5]*

[1]Department of Botany, Sri Venkateswara College, Delhi University South Campus, New Delhi, India.
[2]Department of Education in Science and Mathematics, NCERT-Regional Institute of Education, Mysuru, Karnataka, India.
[3]Department of Agronomy, School of Agriculture, Lovely Professional University, Phagwara, Punjab, India.
[4]Department of Life Sciences, Sri Venkateswara College, Delhi University-South Campus, New Delhi, India.
[5]Department of Biotechnology, Amity University Rajasthan, Jaipur, India.

ARTICLE INFO

Article history:
Received on: 25/07/2025
Accepted on: 06/01/2026
Available online: ***

Key words:
Millets,
Biotechnology,
Genetic transformation,
Bio-fortification.

ABSTRACT

Millets are a resilient and climate-smart alternative to conventional staple crops such as rice, wheat, and maize. Their ability to survive in arid and semi-arid regions, coupled with their resistance to drought, high temperatures, and poor soil conditions, makes them a valuable crop in the face of climate change. In addition, millets require lower inputs, such as water and fertilizers, reducing the environmental footprint of agriculture. They provide significant nutritional benefits and are rich in fiber, essential micronutrients such as iron and calcium. They have a low-glycemic index. The genetic diversity within millet species allows for the development of improved varieties with enhanced stress tolerance and higher yields. By integrating millets into mainstream agriculture and global food systems, policymakers and farmers can enhance food security, mitigate the risks associated with climate change, and promote sustainable agricultural practices. Much work has been done on some millets such as *Eleusine coracana* (Finger millet), *Pennisetum glaucum* (Pearl Millet), *Setaria italica* (Foxtail millet), and *Paspalum scrobiculatum* (Kodo Millet). However, some other millets are not very well researched. The importance of millets in ensuring global food security is widely recognised. India is the highest producer of millets, contributing to 43% of the world's millet production in the year 2023. With an area of 9163754 ha (FAOSTAT data of 2023) under millet cultivation, India is globally well-positioned to be a contributor to the world's food security. This review highlights the significance of millets and recent advancements in biotechnology, with a focus on micropropagation, genetic transformation, and genome sequencing.

1. INTRODUCTION

Cereal grains are the world's most important food source and have a significant role in the human diet. With the recent climate trends and increasing population, it has become essential to identify ways to improve the production of cereals. The term "millet" or minor cereals refers to small-seeded cereals and forage grasses used for food, feed, and forage. They are broadly divided into two categories – major and minor (small) millets. Major millets include cereals such as pearl millet (*Pennisetum glaucum*) and finger millet (*Eleusine coracana*), while minor millets include barnyard millet (*Echinochloa frumentacea*), kodo millet (*Paspalum scrobiculatum*), and little millet (*Panicum miliare*), among others [Table 1]. All millets and cereal crops, as listed in Table 1, belong to the grass family *Poaceae* (Gramineae). The members of this family have narrow leaves, hollow cylindrical stems (known as culms) with clear nodes, leaf sheath covers the stem, and the inflorescence is a spike or panicle. Flowers are small, sessile, bracteate, and zygomorphic with a modified perianth. They typically have two lodicules (reduced perianth parts), three stamens, and a single carpel with a superior, unilocular ovary, and two styles. The fruit is a caryopsis, which is dry, indehiscent where the seed is fused to the fruit wall [1].

In the developing world, malnutrition is a major concern, and most people are habituated to a cereal-based diet. The grains of minor millets are nutritionally superior to rice and wheat [2] as these are rich in dietary fiber, proteins, minerals, and vitamins, and hence these are re-evaluated as Nutri-cereal. Millets can be grown even in poor soil and changing climatic conditions. Among millets, pearl millet is one of the world's most important cereal crops, ranking sixth after wheat, rice, maize, barley, and sorghum [3]. There has been a steady growth

---

*Corresponding Author:
S. L. Kothari,
Department of Biotechnology, Vice President-Amity Science, Technology and Innovation Foundation (ASTIF) Amity University, Rajasthan, Jaipur, India.
E-mail: slkothari28@gmail.com

Table 1: Millet species [1].

Botanical name	Common name	Botanical name	Common name
Brachiaria ramosa	Browntop millet	*Eleusine coracana*	Finger millet
Coix lacryma jobi	Job's tears	*Eragrostis teff*	Teff
Digitaria exilis	Hungry rice	*Panicum miliaceum*	Proso millet
Digitaria ibura	Fonio or Hungry rice	*Panicum miliare*	Little millet
Echinochloa colona	Jungle rice	*Paspalum notatum*	Bahia grass
Echinochloa decompositum	Australian millet	*Paspalum scrobiculatum*	Kodo millet
Echinochloa frumentacea	Japanese barnyard millet	*Pennisetum glaucum*	Pearl millet
Setaria italica	Foxtail millet		

in the production and demand of millets over the years. According to the 2023 report of the US Department of Agriculture, the global production of millets has increased from 26.261 million metric tonnes in 2012 to 31.449 million metric tonnes in 2022, while the area used for millet cultivation has also increased from 27.977 million hectares to 33.125 million hectares between 2012 and 2022. Many new industries and start-ups focusing on millet-based products are emerging, thus increasing the demand and supply for millet manifold.

In their natural form, millets are gluten-free and therefore acceptable for people who suffer from gluten sensitivity. Packed with micronutrients such as iron, calcium, magnesium, and zinc, millets help fight malnutrition, especially in areas with restricted dietary options [4]. Due to their high fiber content, millets are good for gut health and for controlling other diseases such as diabetes because they reduce food's glycemic index. Given that there are micronutrient deficiencies in specific areas, high-quality diets that include millets will enhance health among the population. These crops readily grow under some of the most difficult climatic conditions, such as high temperatures, little rainfall, and poor-quality soils. They have a short growing period, and hence can be slotted into various production programs. Millets, being monocots in nature, possess a fibrous root system composed of distinct root categories that vary in their contributions to root system expansion, branching, and tropism dynamics. These roots also play differential roles in water uptake and transport, collectively influencing the plant's ability to access soil moisture and sustain growth under diverse environmental conditions. All these attributes make millets a strategic crop, especially given the expectation that climate change will lower the yield of regular cereals in several areas [5]. Through targeted initiatives across several African countries, the promotion and cultivation of millets contribute to sustainable agricultural systems. Millets serve as climate-resilient crops capable of maintaining productivity under conditions of heat, drought, and poor soil fertility, thereby supporting food security in regions where climate change is already adversely affecting yields of major cereals.

The rapid increase in global population is intensifying pressure on agricultural systems, necessitating enhanced productivity, resource efficiency, and resilience to meet rising food demand. With staple crops such as rice, wheat, and maize, today's food system is sensitive to abiotic stresses such as drought, flood, and temperature effects. The dependence on some major crops as staple crops across the world poses a significant risk in case of a sudden climate crisis or biotic infestation. Millets, a highly diversified and distinct group of small-seeded cereals, present a strategic intervention for managing these food security challenges. Millets are aspects of ancillary farming in many areas of Africa and Asia and are now emerging as essential tools in reinforcing the worth of agriculture around the world [6].

Biotechnology plays a vital role in enhancing millet yields by developing disease-, pest-, and stress-resistant varieties [7]. Genetic engineering techniques, marker-assisted selection (MAS), and genomics enable scientists to select for better millet yield, quality, and resistance to biotic and/or abiotic stresses. For instance, breeding new millet varieties capable of resisting drought and having higher nutrient density will significantly increase production in areas not suited to high production levels. Biotechnological interventions may also help fortify millets with key micronutrients such as iron, zinc, and Vitamin A. This could be especially valuable in the areas where micronutrient malnutrition rates are relatively high, and a denser addition of vital nutrients to staple crops may benefit a large population. Better bio-accessibility of the nutrients in millets would assist in combating hidden hunger in developing countries [8]. Like most crops planted worldwide, millets struggle against pests and diseases, which cause significant losses. Biotechnological innovation has potential in breeding disease-resistant millet through the determination of the resistance genes and their incorporation into breeding strategies.

Even though the demand for millet has increased, very little attention has been paid to research on millet improvement. Asia and Africa are the biggest producers of millet in the world. With India contributing 43% of the world's millet production in the year 2024, we are very well positioned to be the global suppliers of millets [Figure 1]. This paper has discussed the latest advances in micropropagation, biotechnology, and genetic improvement of millets in the last decade. Although research in this area has not grown at a pace akin to wheat or rice research, the past decade has set a precedent for future research progress.

2. MILLETS FOR CLIMATE SMART AGRICULTURE

Rising carbon emissions are intensifying the greenhouse effect, leading to an increase in the Earth's average surface temperature and contributing to significant climate disruptions. Millets are climate smart as they can grow at higher temperatures on impoverished soil with much less water and humidity as compared to other cereals. They can withstand sudden changes in the average temperatures of the Earth's Surface, making them climate smart. Various studies on better adaptation to climate change developed by millets have been reviewed recently [9]. In general, the C4 grasses dominate natural and agricultural settings due to their resilience to extreme environmental conditions. Millets are a group of small-seeded grasses that are known for their climate-resilient features, including adaptation to a wide range of ecological conditions, lower irrigational requirements, better growth and productivity in low nutrient input conditions, less reliance on synthetic fertilizers, and minimum vulnerability to environmental stresses. Due to domestication and intensive selection, the natural stress tolerance of major cereals has been lost. Since millets were primarily domesticated in the semi-arid regions of sub-Saharan Africa and Asia, where selection favored tolerance to environmental extremes, they are an exception [10]. They have been cultivated for thousands of years in dry and semi-arid regions [11].

In addition to being resistant to drought, millet species such as *Brachiaria ramose* exhibit heat tolerance [10], *Coix lacryma-jobi* has low pH and waterlogging tolerance [12], *Digitaria exilis* is tolerant

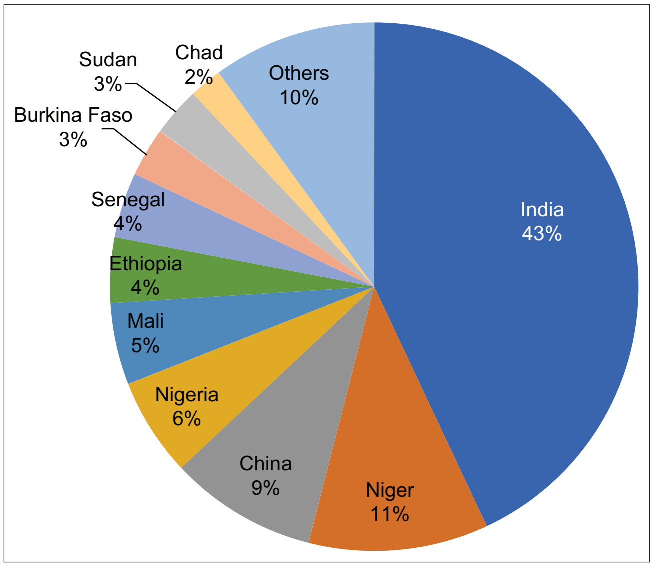

Figure 1: Millet producers of the world in 2024 (U.S. Department of Agriculture, Foreign Agricultural Service [USDA FAS], 2025) [163].

to osmotic stress [13], *Digitaria iburua* is tolerant to poor soil [14], *Echinochloa frumentacea* is stress-tolerant [15], *Pennisetum glaucum* is highly resistant to salinity and heat stress [16], *Setaria italica* is resistant to extreme temperature [17].

P. scrobiculatum L. was analyzed [18] for the comparative responses of salinity stresses induced by various concentrations of NaCl and seawater during seed germination and seedling growth under e*x vitro* conditions. It was found to tolerate up to 250 mM NaCl concentrations. Several studies on abiotic stress tolerance in millets [13,17,19-21] have revealed the remarkable ability of millets to tolerate salinity, drought, and high temperature conditions. With the increased understanding of better adaptation of millet crops to changing climatic conditions, few countries, including China and India, intend to shift their agriculture toward growing more millets. It is estimated that when households return to their pearl millet consumption rates that prevailed in the early-reform period, it could result in a saving of USD 75 m by the Indian Government [22]. The money saved could be reinvested in agriculture to finance climate adaptation/mitigation efforts, contributing to a sustainable food system.

During seasonal shifts, millets give a regular yield while the rest of the crops fail, and thus help feed groups of people who live in such areas. It is, therefore, easy to see why millets are a preferred input in climate-smart agriculture, which integrates a low level of input with the ability to cope with climatic stress [23]. In this regard, European countries and others ought to support millet cultivation as these grains help in avoiding the impacts of climate change on agricultural production to farmers, thereby guaranteeing the food basket under any odds, like climate change. Besides, the climate-smart characteristics of millets include compelling features in promoting crop rotation that enhance the farming system's soil health and biodiversity.

2.1. Water-Efficient and Drought-Tolerant Characteristics of Millets

Water is widely known to be the biggest problem facing agriculture in the modern world, especially in arid and semi-arid areas. Millets are water-efficient crops that use far less water than crops such as wheat and rice [24]. As such, they can be highly recommended for cultivation in any region with low water availability. They can grow in a diminished irrigation frequency and are usually cultivated in rain-fed agriculture. Several physiological and genetic factors have made millet resistant to drought conditions. This includes closure of stomata during water scarcity conditions, a reduction in the size of leaves to reduce transpiration, and osmolyte accumulation to shield cells from a lack of water. Furthermore, millets are phenotypically plastic to the development period in that they can quickly adapt to the short growing periods necessary in areas that receive seasonal rains [25]. However, higher levels of drought stress markedly reduced germination and hindered early seedling development in finger millet varieties and foxtail millet [26,27]. Drought stress led to a significant decline in grain yield and water use efficiency (WUE) during the ear emergence stage in Proso millet [28]. Pearl millet (*P. glaucum*) suffers considerable yield penalties under drought stress, particularly when water deficit coincides with reproductive stages. Terminal drought during flowering and grain filling has been reported to reduce grain yield by up to 65% and straw yield by 53%, mainly due to reduced panicle development and biomass production [29,30].

2.2. Role of Millets in Reducing Greenhouse Gas (GHG) Emissions and Supporting Sustainability

Millets are less carbon-intensive than crops such as rice, which produce much methane during their growth cycle. Ample adaptation to arid conditions reduces dependence on power-intensive irrigation systems and fertilizers, which form the primary sources of GHG emissions in the farming industry [31]. Moreover, millets are generally produced using traditional methods of cultivation, which are more sustainable and tend to avoid synthetic inputs. They also play the role of earning carbon credits by improving and enhancing soil conservation and fighting land degradation. Their root structure improves the soil's physical characteristics and reduces erosion rates, in addition to the addition of organic matter and nutrient cycling resulting from their inclusion in crop rotations. More so, the use of millet promotes agricultural practices that create sustainable food systems. This will enable farmers to grow millet and other crops in crop diversions to avoid monoculture, leading to poor soil structure and increased GHG emissions [32].

The original green revolution led to an increased dependence on paddy cultivation. This posed immense pressure on groundwater resources, leading to their depletion. The Indian government has been actively aiming to bring down areas under paddy cultivation since 2013–2014 through the Crop Diversification Program and promote millets (and pulses and oilseeds) on these farms [33]. Promotion of the cultivation and consumption of millets, coupled with research and breeding programs focused on climate resilience, can play a vital role in advancing climate-smart agriculture and building more sustainable food systems. Khangar and Monhansundari, in 2024 [34], in their studies on the environmental impact of different crops, found that Maize had an environmental degradation score of 4993.50, sorghum 2276.34, and millets had as low as 126.55. Pearl millet is understood to have increased WUE, nitrogen use efficiency, and potential for carbon sequestration [35]. Since millets are C4 plants, they aid in climate change mitigation by efficiently fixing carbon dioxide and releasing oxygen, thereby reducing GHG emissions [36].

2.3. Adaptation of Millets to Diverse Agro-Ecological Conditions

The fact that the millets survive under various conditions remains their most significant asset [24]. They are drought–hardy grains that can grow well in areas where the annual rainfall may be 300–400 mm. Moreover, they can withstand high temperatures and germinate in potentially infertile soils [3]. Due to their low input density, they are well-suited for cultivation by small farmers, mainly when resources are severely restricted. Millets have tiny seeds and require short days to mature; it takes some species as little as 60–90 days. This characteristic enables them to be produced with short rainfall durations, and they outcompete all other crops in water and land requirements. They are usually resistant to many diseases and pests commonly known to affect other cereal crops. Regarding climate change resilience, millets can cope with varying and often unpredictable weather conditions ranging from droughts to heat waves; hence, they have the potential to be embraced as a crop for an improved climate change-resistant farming system [38].

3. NUTRITIONAL SUPERIORITY AND MEDICINAL VALUE OF MILLETS

Millets are a traditional staple food in dryland regions of the world. They are nutri-cereals with high nutrient content, including protein, essential fatty acids, dietary fiber, Vitamin B, and minerals such as calcium, iron, zinc, potassium, and magnesium.

3.1. Global Importance of Millet Species Diversity, Health Benefits, and Nutritional Value of Millets

Millet foods are characterized as potential prebiotics as they can enhance the viability or functionality of probiotics with significant health benefits. The different species of millets are rich in various nutrients, such as *Brachiaria ramosa* is rich in protein content, copper, potassium [39]; *C. lacryma-jobi* has high-protein content, triacylglycerols, Vitamin E, calcium and essential amino acids such as leucine, arginine, lysine, and tyrosine [40]; *D. exilis* has low-glycemic index, high-protein content, Vitamin B, zinc, and iron; *D. iburua* and *Echinochloa colona* are both gluten free and have high polyunsaturated fatty acid content [14,41]. *Eragrostis teff* is also gluten-free, has a high content of unsaturated fatty acids, and is rich in potassium (K), phosphorus (P), magnesium (Mg), calcium (Ca), sodium (Na), zinc (Zn), and iron (Fe) [42]. *P. glaucum* has higher iron and zinc content, polyphenols, lipids, and fibres [43]. *S. italica* has a low-glycemic index and is rich in essential amino acids, saturated and unsaturated fatty acids, Vitamins A and B1, tannins, and phytic acid [44]. *Paspalum notatum* is a rich source of potassium and phosphorus and contains low-to-medium crude protein and a high amount of lignin [45]. *Panicum miliaceum* is gluten-free, low in glycemic index, and has high lecithin, vitamins, and minerals such as phosphorus, manganese, magnesium, calcium, and Vitamin B-3 [37,46]. A comparative account of the proximate composition of proteins, fats, carbohydrates, vitamins, iron, and calcium can be seen in Table 2. The protein component of *P. miliare* is comparable to wheat and higher than that of rice and maize. The total dietary fiber composition of *Eleusine* is almost 3 times higher than that of rice. Ragi is also exceptionally rich in calcium and vitamins of the B family [Table 2 and Figure 2].

Apart from being nutritionally rich, millets have medicinal importance as well. *P. miliaceum* has gluten-free grain, and therefore, it is suitable for people with coeliac disease and gluten intolerance. It is an effective alternative to wheat and wheat products. It is rich in phytochemicals, including phytic acid, which is believed to lower cholesterol and phytate and is associated with reducing cancer risks, along with phenolic and benzoic acids. *S. italica* L. possesses hypolipidemic and antioxidant characteristics. It is suitable for individuals suffering from diabetes mellitus due to its low-glycemic index [47]. *Coix lacryma-jobi* L. and its extracts are rich in 30 ingredients with more than 20 health effects based on human and animal or cell cultures. Its seeds contain phenols, flavonoids, polysaccharides, proteins, fibers, vitamins, and oils. *Coix* is sold as Kanglaite in China as an anticancer drug. It has potent chemical constituents that inhibit enzymes of cyclooxygenase, fatty acid synthase, matrix metalloproteinases, and liver cholesterol synthesis. They are anti-cancerous, anti-inflammatory, anti-obesity, anti-diabetes, osteoporosis preventive, analgesic, neuroprotectant, and suitable for the treatment of gout arthritis [40].

4. BIOTECHNOLOGICAL INTERVENTIONS IN MILLETS

Despite all the competitive advantages that millets have vis-à-vis the other cereal crops, biotechnological approaches to improving millet production and yields can play a vital role in increasing millet production, climate change, and food security [153]. Techniques such as micropropagation, genetic transformation, and genome sequencing have helped enhance qualitative attributes and quantitative yields of millets [Figure 3] [48].

4.1. Micropropagation Techniques and Applications for Rapid Multiplication

In the past, micropropagation or *in vitro* regeneration of millets was less commonly studied due to two problems. Millets have been considered as neglected food sources since the colonial era due to the prevailing preference for expensive staples such as rice and wheat. This shift in preference can be attributed to the growing need for other crops such as cotton, wheat, and oilseeds. Furthermore, due to its technical complexity, high cost, and requirement for painstaking precision, micropropagation remains accessible only to a few dedicated

Table 2: Proximate nutritional composition.

Food grain	Protein	Fat	Total dietary fiber	Carbohydrates	Vitamin B1	Vitamin B2	Vitamin B3	Calcium	Iron
Wheat (*Triticum aestivum)*	10.6	1.53	11.36	64.17	0.42	0.15	2.37	20.4	1.77
Rice (*Oryza sativa)*- parboiled. Milled	7.81	**0.55**	3.74	**77.16**	0.17	0.06	2.51	8.11	0.72
Maize (*Zea mays*)	8.8	3.77	**12.24**	64.77	0.33	0.09	**2.69**	8.91	2.49
Bajra (*Pennisetum typhoideum)*	**10.96**	5.43	11.49	61.29	0.25	0.2	0.86	27.35	**6.43**
Jowar (*Sorghum vulgare*)	9.97	1.73	10.22	67.68	0.35	0.14	2.1	27.6	3.95
Finger millet (*Eleusine coracana)*	7.16	1.92	11.18	66.82	**0.37**	**0.17**	1.34	**364**	4.62
Little Millet (*Panicum miliare*)	10.13	3.89	7.72	65.55	0.26	0.05	1.29	16.06	1.2
Kodo millet (*Paspalum scrobiculatum)*	8.92	2.55	6.39	66.2	0.29	0.2	1.49	15.37	2.36

All values are expressed per 100 g edible portion; Source: Indian Food Composition Tables-NIN,2017. The highest values are given in bold text and resourceful horticulturists. Nevertheless, during the last decade, a considerable number of scientists, botanists, and horticulturists had initiated research efforts in the field of millet tissue culture or micropropagation to enhance the development of the superfood millet. The research not only revitalized the cultivation of millets but also brought attention to previously overlooked or neglected characteristics that could enhance the quality of superfoods. Micropropagation is a plant tissue culture technique that has the potential to increase the supply of millet planting materials rapidly [52]. Different explant materials such as mature embryos, immature embryos, leaf, stem, and caryopsis have been used for raising regenerable cultures in millets [Table 3]. The cultured explants usually follow an indirect regeneration pathway where there is callus formation first, and then plant regeneration occurs through either somatic embryogenesis or organogenesis. The explants are cultured on a nutrient medium enriched with plant growth regulators. The concentrations of these growth regulators are critical in determining the growth differentiation of the plant tissues [49,54]. For example, an increase in the content of cytokinins may promote shoot formation, whereas auxins are ordinarily employed to encourage rooting. Table 3 gives an overview of the different kinds of PGRs and growth supplements that have been used in the micropropagation studies of millets. In some cases, like *E. coracana*, an enlarged apical dome forms, and then shoot buds are differentiated on the entire dome surface [57,58]. Micropropagation accelerates the process of multiplication and dramatically minimizes the time required to bring into production, large quantity of planting material. This, in turn, is important in addressing the challenges of smallholder farmers and addressing food security around the globe. Moreover, using disease-free tissue cultures, farmers abstain from planting pathogens that often attack millet grain, which are predisposing factors for the crop's vulnerability [55].

Micropropagation and plant regeneration from tissue cultures of millets faced several challenges due to their recalcitrant nature and genotype dependence toward efficient plant regeneration. However, plant regeneration studies in the past few decades have shown that through the use of immature embryos and seeds as the starting material and use of 2,4-D as the growth regulator, most of the small millets have been regenerated in tissue cultures [49], In addition, the nutrient manipulation (use of higher amounts of heavy metals such as Cu) has improved the regeneration efficiency of the millets to a great extent [50,51].

The earliest attempt to culture cereal and millet dates to the 1970s, when successful callus formation and plant regeneration were reported in minor millets [56]. Different combinations of plant growth regulators alongside additives such as sugars, amino acids, and charcoal were used to study their impact on plant regeneration in millets [Table 3]. In some studies, on *E. coracana*, it was also understood that the inherent compositions of phytonutrients and phyto-hormones in different genotypes also significantly impact the *in vitro* response of these plants [59]. While considerable work on micropropagation studies has been done on some millets, plants such as *B. ramosa* (Browntop millet), *D. exilis* (Fonio), *D. iburua* (Black fonio), *E. colona* (Jungle rice), and *Panicum decompositum* (Australian millets) have received little attention in scientific studies due to their relatively lesser-known advantages and health benefits.

Micropropagation affords several considerable benefits in millet production, including the production of disease-free planting material. Usually, through propagating, disease-causing agents are spread, affecting crop production [52]. Conventional vegetative propagation methods are often time-consuming and typically require large areas of land. In contrast, micropropagation enables the large-scale production of thousands of genetically uniform plantlets within a relatively short period, thereby substantially enhancing the availability of planting material. This rapid multiplication capacity is especially valuable in regions where particular millet varieties possess localized importance, allowing farmers to meet specific varietal demands promptly and efficiently

4.2. Genetic Transformation of Millets

Genetic improvements in millets involve the application of various breeding techniques and molecular tools to enhance the desirable traits of millet crops. Some of the key benefits of genetic transformation of millets include yield improvement, disease resistance, drought tolerance, enhanced nutritional quality, improved seed size and quality, temperature and soil adaptability, resilience to climate change,

Table 3: *In vitro* plant regeneration in millets using a combination of different plant growth regulators and other additives.

Plant species	Explant used	PGRs and other additives used for callus induction and/or plant regeneration	References
Coix lacryma-jobi	Anther	2,4-D, Kinetin, Indole Acetic Acid, Agnihotra Ash, and Cow Dung Ash	[60,61]
Digitaria exilis	Stem (culm), Leaf	2,4-D, BAP, GA_3	[62]
Echinochloa frumentacea	Caryopsis, Seed	2, 4-D, NAA, IBA, kinetin, BAP, and GA_3	[63]
Eleusine coracana	Mature seed, Shoot apex, Mesocotyl, Leaf base, Shoot tips, and Inflorescences	2,4-D; 6-BAP; GA_3; NAA; Picloram; Spermidine; Kinetin and ABA	[59,64-75]
Eragrostis tef	Immature embryo, Mature embryo, endosperm, scutellum	K99 medium with maltose, glutamine and 2,4-D, α-naphthaleneacetic acid, L-proline, casamino acid, benzyladenine (BA)	[76-78]
Panicum miliaceum	Immature and mature embryo, Young leaf base, mesocotyl, seeds, cotyledon	2,4-D, Kinetin, 6-BA, and NAA	[79,80]
Paspalum notatum	Leaflets, Mature seed and shoot meristem	2,4-D; BA, Nacl, colchicine	[81,82]
Paspalum scrobiculatum	Mature embryo	2,4-D; $AgNO_3$	[83]
Pennisetum glaucum	Mature embryo, Shoot tip, Immature inflorescence, and leaf base	Kinetin; BAP; IAA; Thidiazuron; 2,4-D	[84-87]
Setaria italica	Basal shoot, Shoot tip, Seeds, Leaf base	2,4-D; Kinetin; BAP; NAA, Amino acids (proline, glycine, cysteine); charcoal, rice husk charcoal and cocopeat, cefotaxime	[88-91]

2,4-D-2,4 dichlorophenoxyacetic acid, BAP: 6-benzylaminopurine, GA3: Gibberellic acid, NAA: Naphthalene acetic acid, IBA: Indole butyric acid, ABA: Abscisic acid.

biotic, and abiotic stress resistance, ultimately contributing to global food security [92]. For the biotechnological improvement of various millets, *Agrobacterium*-mediated genetic transformation has been the primary and most preferred method of transformation due to its wide host range, stable T-DNA integration, relatively low transgenic copy number, and minimal equipment use [15,93]. Historically, monocots have been difficult to transform using *Agrobacterium* as compared to dicots due to anatomical differences, limited wound response, and vir gene-inducing compounds. The use of other genetic improvement techniques, such as biolistic and microprojectile bombardment, has been limited. There have been numerous studies on the transformation of pearl millet, kodo millet, foxtail millet, etc. [Table 4]; however, there is a scope for further studies, since millet transformation is not very well researched.

Although *Agrobacterium*-mediated and microprojectile bombardment are methods of choice for genetic transformation studies in millets, however, certain novel methods have been used to induce variations in some millets. Seeds of *D. exilis* were exposed to gamma irradiation (20Gy, 40Gy, 80Gy, and 100Gy) from a 60Co source, and these seeds were sown for evaluation. It was found that 80Gy or a slightly low dosage form of gamma irradiation using cobalt could be utilized to increase variability and yield in *D. exilis* [94]. Experiments to investigate the effects of colchicine and gamma rays in the improvement of *D. exilis* indicated that colchicine improves the sizes of the traits of interest such as height, leaf area, diameter, and weights of the seeds while gamma radiation improve the number of the selected traits such as leaf number, number of tillers and spikes, and number of seeds/spikes [95]. An insight into the potential of advanced tools such as CRISPR-Cas for use by plant biologists to improve stress resilience, modify plant architecture, and improve productivity has been proposed [96]. Application of this cutting-edge technology in underutilized/orphan crops may lead to several benefits, like conferring lodging resistance in tef [97]. Sequencing of *E. teff* genome for marker-assisted breeding sheds light on molecular mechanisms explaining its superior nutritional and agronomic properties and making the genomic resource publicly accessible [98].

E. coracana and *P. glaucum* are among the well-researched millets in terms of the establishment of a genetic transformation protocol and standardization of the various factors that may affect the efficiency of regeneration [Table 4]. The most widely used *Agrobacterium* strain for millet transformations is LBA4404, EHA101, and derivatives of EHA101 (viz., EHA105, AGL0, and AGL1). Optimization of genetic transformation protocol has been reported in *D. exilis*, *Echinochloa* spp., *E. coracana*, *P. notatum*, *P. scrobiculatum*, and *S. italica,* to name a few. The following factors must be taken into account while establishing a robust transformation protocol namely, appropriate promoters, proper explants, and transfer mechanisms. However, reports of the transfer of genes from the tertiary gene pool for millet improvement are very few.

4.2.1. Stress tolerance in millets: A biotechnological perspective

Molecular technologies offer substantial means to create stress-tolerant millet varieties capable of withstanding these stress factors without penalty in yield or nutritional value [117]. Biotechnological tools such as genetic engineering, molecular MAS, and genetic transformation offer clear advantages over traditional breeding methods in terms of precision in the choice of genes to be used or modified to confer stress tolerance characteristics [118]. Overexpressing genes that are used in osmotic regulation, mechanisms through enzymes in the proline biosynthesis pathway may be used for enhancing plant growth under water-deficit conditions and hence contribute to drought tolerance [119].

Different abiotic stresses, especially drought, salinity, and heat, are significant constraints to crop production, especially in arid and semi-arid areas, which are the main growing areas for millets. Manipulation of stress-responsive pathways has been another approach in the millet biotechnology [120].

Drought Tolerance: Water stress, especially drought, is one of the most important abiotic stresses. In their natural habitats, millets are more drought-resistant than many other cereal crops because they use water sparingly and grow on marginal soils. Nevertheless, given more frequent and severe drought incidents due to climate change, improving drought tolerance further is an attractive possibility. The genes manipulated in millets include the Dehydration-Responsive Element-Binding Protein 1A gene. This gene triggers a string of stress responses that enhance the plant’s capacity when subjected to a short duration of water deficits. Furthermore, the enhanced expression of aquaporin genes involved in water transport in the plant tissues has been reported significant improvement in drought tolerance in the genetically transformed millets [121].

Salinity Tolerance: The choice of biotechnological strategies for salinity tolerance improvement in millets is based on the ability

Table 4: Genetic transformation in millets.

Plant species	Gene introduced	Desirable trait/outcome	References
Digitaria exilis	hpt, nptII, gus	Hygromycin resistance	[62,99]
Echinochloa spp.	gus	Transient GUS activity in the presence of the Ubiquitin 1 promoter from Maize	[100]
Eleusine coracana	nptII, mutant α-tubulin (TUAml), hptII, gus, OsSOS1, Erianthus arundinaceous DREB2 (EaDREB2) transcription factor, PDH45	dinitroaniline-resistance, transient GUS activity, high salt tolerance, high drought tolerance	[101-107]
Eragrostis tef	GA inactivating gene- PcGA2ox	Semi-dwarf phenotype	[108]
Paspalum notatum	Npt II, bar, cinnamyl alcohol dehydrogenase gene.	Transient GUS activity, Reduction of lignin content	[45,109]
Paspalum scrobiculatum	Gus	Transient GUS activity,	[110]
Pennisetum glaucum	antimicrobial peptide magainin gene, *acetolactate synthase (ALS)* gene, hptII, GUS	Basta-tolerant putative transformed plants, Resistance to Chlorsulfuron	[111-114]
Setaria italica	HptII, Lysine-rich protein encoding gene SBgLR from potato	Hygromycin resistance, Lysine-rich protein, Transient GUS activity,	[115,116]

of ion transporters and osmo-protectants to stabilize the cell under saline conditions. For instance, overexpression of NHX1, a gene encoding a sodium/hydrogen antiporter, is known to enhance salt tolerance. It assists in pumping sodium ions into vacuoles where they are sequestered. Similarly, genes encoding enzymes involved in the biosynthesis of compatible solutes, such as glycine betaine, are considered prime targets for incorporation to enhance osmotic adjustment in millets. Such improvements can enable the grains to germinate and grow more effectively under saline conditions [122].

Heat Tolerance: Heat stress is regarded as one of the most emergent factors influencing agricultural production in the condition of escalating global temperatures, as it is critical for the countries of the tropical and subtropic zones. Temperature influences photosynthesis, stability of proteins, and water relations in plants. Biotechnological strategies have used HSPs and HsfA1 transcription factors that control the heat stress response and enhance heat tolerance in millets [123]. VHSPs are heat shock proteins that prevent the denaturation of proteins during heat stress. The introduction of genes coding for HSPs and heat-tolerant transcription factors and breeding for higher levels of HSPs has been demonstrated to have considerable success in improving the heat tolerance of millets without adversely reducing yields during prolonged heat stress.

Stress-tolerant millet varieties are not only a requirement for food production sustenance but also an important factor in climate change mitigation and sustainable agriculture. With climate change leading to changes in rainfall intensity and frequency of storms, coupled with an increase in instances of enhanced rates of soil erosion, crops such as millets will define food security in the times to come.

4.3. Genome Sequencing and Its Role in Understanding Genetic Diversity

Genome sequencing of millets has brought a change in plant breeding because of the information that is made available about their genetic variability. Appreciation of this diversity is essential in improving crop resistance and flexibility in the face of environmental changes. The importance of genome sequencing is to locate markers for determining the selected properties [124]. Advancements in next-generation sequencing technologies, which have significantly reduced the time and cost of sequencing, have enabled the precise identification of genes associated with desirable traits. This has facilitated the development of markers for use in MAS, allowing plant breeders to efficiently select genotypes with favorable characteristics based on their genetic profiles [125, 154]. Moreover, genome sequencing provides information about millet species' phylogenetic relationships and genetic structure. This knowledge helps breeders understand the outcomes of gene blends, which means that better varieties of crops can be produced in terms of yield, dietetic value, and resistance to diseases [126].

Genome sequences of sorghum, pearl millet (major millets), fonio millet, foxtail millet,kodo millet, job's tear, barnyard millet, finger millet, proso millet, and tef (minor millets) are now available. Transcriptome studies can help in the identification of differentially expressed genes, mine genes induced in a particular stress, and develop several molecular markers for all plants, including millets [127-129]. *P. glaucum*, is unveiled to have a complex genetic structure. It has about 2.5 billion bases. The presence of such genomic data enables comparative genomics, which helps in the identification of orthologs and core synthetic genes from different millets and related crops. The findings and knowledge acquired from such studies help frame breeding strategies to improve the resistance and productivity of the millet varieties by identifying alleles with desirable traits [130].

4.3.1. Identification of genes controlling important traits and development of molecular markers

A major outcome of millet genome sequencing has been the ability to identify genes associated with key agronomic traits, thereby enabling more targeted approaches to crop improvement. For instance, the genes responsible for phytochemicals resisting pests and diseases have been identified, offering potential transformations. Moreover, the corresponding genes for abiotic stresses such as drought and salinity, can be identified, which can be the basis for creating new stress-tolerant millet varieties [131]. Another important achievement of genomic studies is the identification of quantitative trait loci (QTLs), which are genomic regions associated with the expression of specific traits. Mapping these QTLs onto the genome enables the identification of genetic factors governing yield, disease resistance, nutritional attributes such as protein content, and other agronomically important traits. Understanding the location and effects of QTLs facilitates the development of molecular markers linked to these traits, thereby supporting breeders in the creation of improved millet varieties. Microsatellites, simple sequence repeats (SSRs), and single-nucleotide polymorphisms (SNPs) are other molecular markers that have become significant tools in millet breeding. These markers offer opportunities to estimate the amount of genetic variation, positioning of desired traits, and identification of outstanding genotypes [132]. For example, SSR markers have been used to show genetic relatedness in different millet accessions to guide breeders in selecting appropriate parents for crosses.

4.3.2. Utilization of genomic information for MAS and breeding programs

Using information from the genomic method in MAS is a revolutionary improvement in millet breeding programs [133]. In millet breeding programs, MAS can be used to select desirable attributes, including drought stress, pest resistance, and grain composition. This targeted selection also dramatically minimizes the time and resources needed to generate better millet varieties. Furthermore, it is possible to use genomic information to incorporate the strategies of genomic selection (GS) that allow the assessment of all the potential breeding candidates. GS may sometimes be more informative than MAS since it can estimate multiple traits simultaneously [134]. The sequencing data accrued can also be used to improve millet's nutritional attributes through breeding exercises. The initial approaches towards improving millet yield and stability are the knowledge of genes that regulate desirable agronomic characteristics and the generation of molecular markers [135]. For instance, the genetic traits help researchers screen for markers that contribute directly to thermotolerance generation using naturally heat-tolerant millet genotypes. Such markers can then be used to develop improved varieties that retain high productivity and heat stress tolerance [136].

Unfortunately, the transcriptome datasets of millets have not been adequately explored to find genes associated with traits such as climate resilience, nutrient enrichment, and crop improvement.

4.3.3. Genome resources in major versus minor millets

Major millets such as sorghum (*Sorghum bicolor*) and pearl millet (*P. glaucum*) possess some of the most advanced genomic resources among small-grained cereals. Sorghum was one of the earliest C_4 crops to have a high-quality reference genome, enabling detailed studies on comparative genomics and genome-wide association for yield, drought

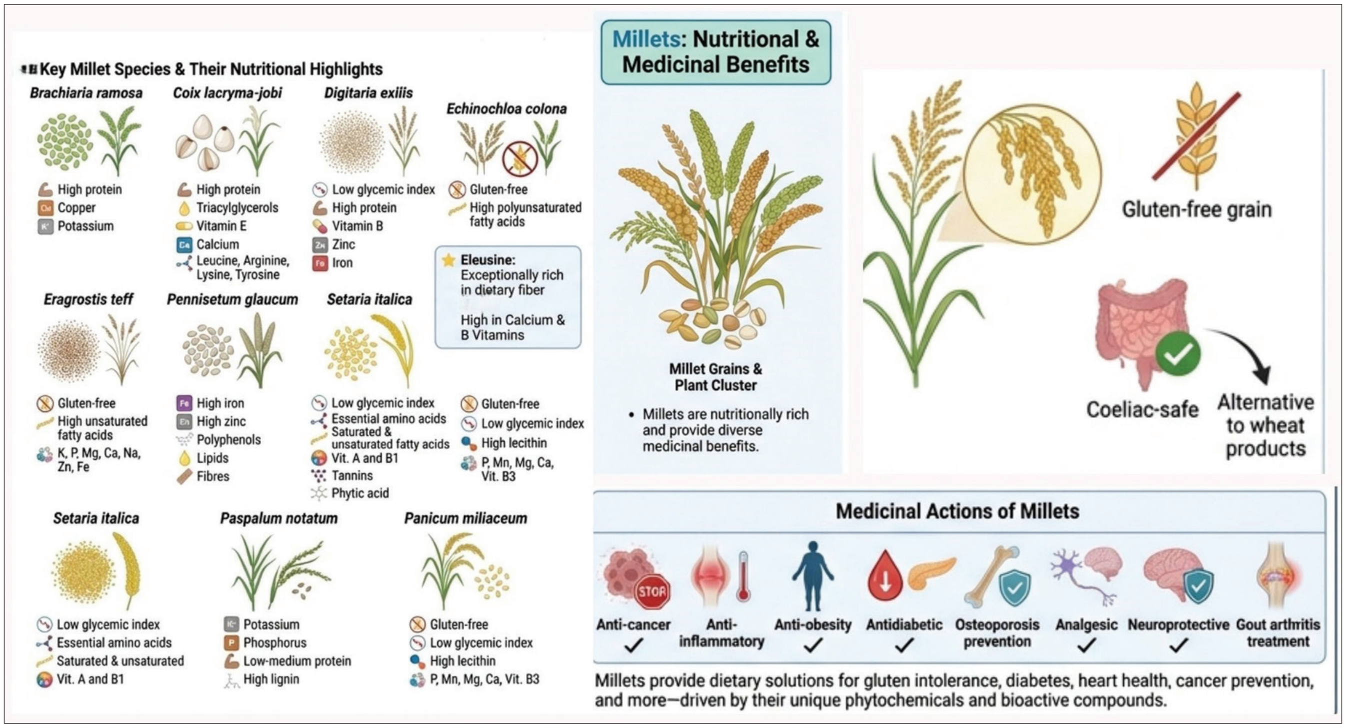

Figure 2: Overview of nutritional and medicinal benefits of millets (Figure prepared using Figure Labs).

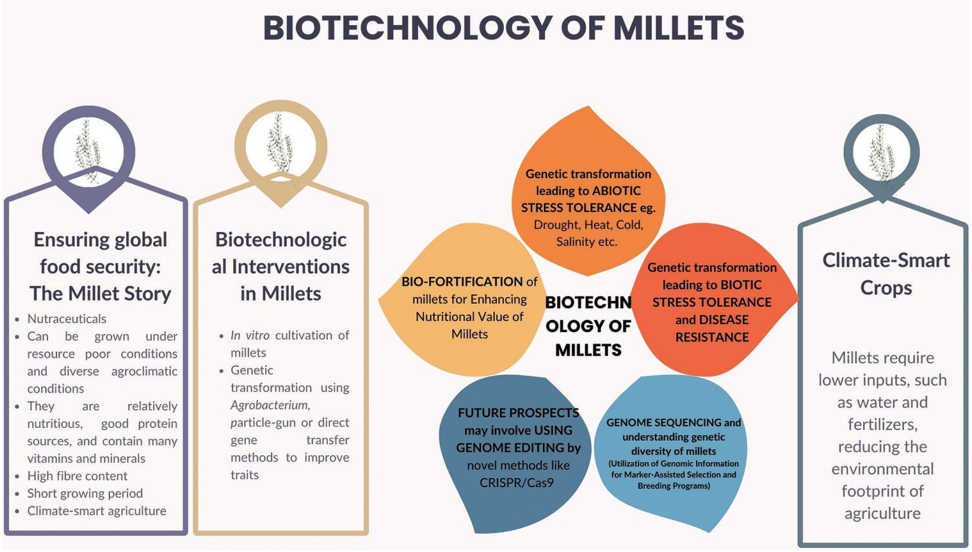

Figure 3: Biotechnological approaches that help in enhancing the production of millets.

tolerance, and biotic stress resistance [156,157]. Pearl millet possesses a large and highly heterozygous genome. Its sequencing has led to the identification of alleles associated with heat adaptation, drought tolerance, and micronutrient content such as iron and zinc [158,159]. These genomic resources have enabled the routine use of high-density SNP markers, GS, and molecular breeding pipelines in major millets.

The genomic resources for minor millets, however, are more fragmented in nature. Foxtail millet (*S. italica*) is the best-characterized among them, with a well-annotated reference genome and growing pan-genome datasets, positioning it as a model system for millet research [160,161]. Finger millet (*E. coracana*) has a sequenced allotetraploid genome. Other minor millets, including proso millet (*P. miliaceum*), little millet, and kodo millet (*P. scrobiculatum*), have only recently obtained draft genome assemblies or transcriptome resources, restricting large-scale GWAS and comparative studies. Overall, while pan-genomics initiatives are beginning to emerge for minor millets, the lack of fully annotated genomes and well-characterized diversity panels remains a key limitation.

In minor millets, biotechnology advances are emerging but remain less widespread. Transcriptome profiling and comparative genomics have been widely used to identify candidate genes for abiotic stress tolerance, nutritional quality, and flowering time, particularly in foxtail and finger millet [162]. However, the application of genome editing technologies, such as CRISPR/Cas9, is still limited due to inefficient regeneration and transformation

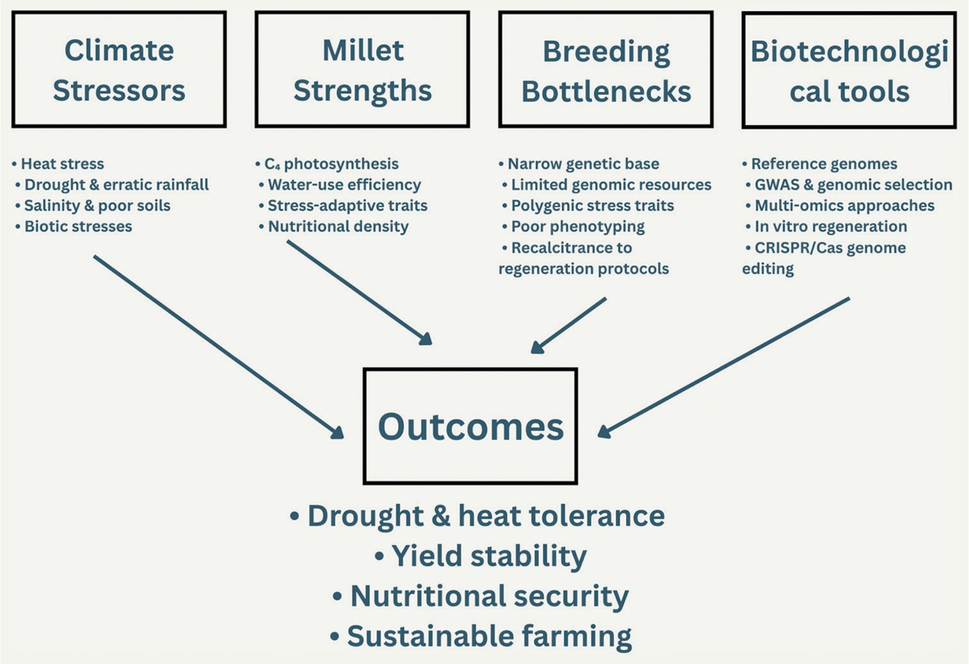

Figure 4: Model showing how climate change pressures interact with breeding bottlenecks in millets and how genomics and biotechnological tools enable accelerated development of improved millet varieties.

protocols. Successful *Agrobacterium*-mediated transformation and CRISPR-based editing have been successfully demonstrated in foxtail millet [162]. For other minor millets, transformation systems are still being studied, constraining the translation of genomic information into precise genetic improvement. Strengthening tissue culture, regeneration, and editing platforms is therefore essential to fully exploit genomic data for climate-resilient and nutritionally enhanced millet varieties.

4.4. Genetic Engineering for Improving Millet Productivity

Genome editing has been accomplished in many crop plants, including rice, wheat, maize, and barley [137], but it remains very limited in millets, although its potential in improving the millet crops to thrive best in changing climate conditions has been shown in foxtail millet [138]. Genome editing can target specific functional genes, which have been identified through sequencing and structural genomic approaches such as zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs), and the CRISPR/Cas system [139]. Novel genome-editing approaches such as CRISPR/Cas9 have emerged, enabling highly precise modifications to specific genomic regions without the introduction of foreign DNA into the organism [140,141]. In millets, the use of CRISPR has enabled the introduction of genes relating to ROS scavenging to be edited so that the plants can handle oxidative stress (generally associated with drought and heat stress) effectively [142]. These edited varieties have higher stress tolerance. CRISPR-Cas9-mediated editing of SiEPF2 in foxtail millet (*S. italica*), a drought-tolerant crop critical for food security, produced two allelic mutants. Functional analysis revealed that SiEPF2 regulates stomatal density, thereby enhancing drought tolerance and panicle development, influencing yield [143].

Further, the proposed omics approach, including genomics, transcriptomics, proteomics, and metabolomics, will help understand the molecular aspects of essential traits in millet. As climate change increasingly threatens global food production through its adverse impacts on agriculture, the development of transgenic millet varieties will play a crucial role in sustaining yields and enhancing resilience. Furthermore, public awareness and acceptance of genetically modified (GM) crops remain essential for the effective deployment and adoption of these technologies [144].

5. BIO-FORTIFICATION OF MILLETS

5.1. Strategies for Enhancing Nutritional Value of Millets through Biofortification

Efforts to biofortify aim to increase the micronutrient density of these crops, especially iron, zinc, and vitamins. Possible strategies to do this may be classified according to traditional breeding techniques, biotechnology, and management practices. The main technique used for biofortification includes conventional breeding, in which millet varieties with higher nutrient densities are naturally crossed [145]. This method is relatively cheap and easy to implement, and hence would most benefit smallholder farmers in the developing world. Genetic modification also improves nutrient content in millets and is even preferable than the previous method. For example, genes regulating the uptake and accumulation of iron or zinc can be up-regulated, enabling edible plant tissues to accumulate higher concentrations of these micronutrients while remaining safe for human consumption. Although this method can significantly improve nutrient content, doing so raises issues of regulation, ethics, and consumer acceptance before it can be implemented [146]. It is also important to recognize that appropriate agronomic practices play a key role in biofortification. The micronutrient content of millet grains can be enhanced through the application of micronutrient-enriched fertilizers. This approach is particularly effective for elements such as zinc and selenium, whose uptake is often limited by their low availability in the soil. However, the long-term success of this strategy depends on consistent access to and supply of fortified fertilizers for farmers [147].

Millet bio-fortification is a viable option for meeting micronutrient gaps when access to various diets or supplements is a challenge. Indeed, since millets are consumed by many communities in the developing world, such as South Africa and South Asia, improving the nutritional value of these grains can literally and directly address human health requirements in those regions. Iron and zinc have been the primary targets for nutritional biofortification in millet genotypes because of the low intake of these micronutrients in most developing nations. Iron deficiency causes anemia and negatively impacts learning ability and, therefore, productivity, while zinc deficiency compromises the immune system and increases the client's vulnerability to infections, in addition to stunted growth. Pearl millet, for instance, has been a focus of iron bio-fortification given that the grain is widely grown in arid areas where anemia is rife. Naturally occurring varieties are liberal in iron, and these have been used to develop varieties that contain up to 70% more iron than ordinary varieties. Intake of this improved millet daily can strongly complement the daily requirement of iron in an individual's diet [148,149]. Millet (finger millet, foxtail millet, and pearl millet) varieties enriched in zinc have been produced through conventional selection methods and genetic engineering; the zinc level in some has been boosted by 1.5–2 times. This fortified millet can help combat zinc deficiency, especially in an area where zinc is proven to cause poor immune systems and high child mortality [150].

Biofortification efforts have also targeted vitamins, such as Vitamin A, by enhancing β-carotene content. Molecular biotechnology techniques have been used to introduce genes involved in the biosynthetic pathway of β-carotene into millet. Although these approaches are in their nascent stages, they hold significant potential for addressing Vitamin A deficiency, a major public health concern responsible for preventable blindness in young children [151,152, 155].

Besides being essential for coeliac disease patients due to the lack of gluten and for diabetes patients due to low-glycemic index, this grain has even more extensive beneficial effects on public health.

6. CONCLUSION

Millets are gaining increasing recognition because they are capable of addressing various global challenges related to food security, nutrition, and sustainable agriculture. The United Nations declared 2023 as the International Year of Millets to raise awareness about the benefits of these small-grain cereals and promote their cultivation and consumption. The declaration was made to highlight the nutritional, environmental, and cultural benefits of millets and to encourage their role in sustainable agriculture and food systems. Millets have traditionally been grown in resource poor areas of the world and research focus on millet improvement was limited. Although *in vitro* culture techniques were developed quite early for all the millet species, the transformation of millets has so far lagged in comparison to significant cereals (wheat, rice, maize, and barley). Integrating biotechnology into the current crop improvement programs with traditional breeding approaches could be one of the most effective strategies for achieving significant improvements in millet cultivation. Selective plant breeding has been done by crossbreeding different plant species to give the required characteristics, such as disease resistance, higher yield, and stress tolerance. However, this process is time consuming and is confined mainly by the number of incidental desirable characters in a particular species. It can be noted that the application of biotechnology as a complementary tool along with basic selection and breeding techniques is essential for efficient production, which meets the current demands of world food security. Integrating modern approaches, like the use of molecular markers, the CRISPR technique, and the conventional breeding approach may lead to the development of crops with high yields and improved stress tolerance. For example, the ability to grow crops in arid conditions is one area that interests both biotechnology and breeding. Using Marker Assisted Selection (MAS) and Genomic Selection, breeders can identify plants carrying genes for abiotic stress tolerance viz. water stress. Selective breeding can then be followed up with genetic engineering to other genes for other desired characteristics, like water use productivity or deeper root structure to increase drought resistance. In the same way, genetic engineering techniques can be employed to enhance the nutritional value of crops and thereby help control chronic problems such as malnutrition and shortages of micronutrients in many countries. Bio-fortification, that is, the ability to improve the nutritional quality of crops through biotechnology and breeding techniques, including increases in iron, zinc, or vitamins is also an area of significant potential [Figure 4].

While there has been increasing interest and research on millets in recent years, it is true that compared to major staple crops such as rice, wheat, and maize, millets have historically received less attention. However, the importance of millets is being recognized, and efforts are underway to fill the research gaps. Most of the millets are not economically important to developed countries, so scarcity of research funding has always been a problem. Under the circumstances of climate change and predicted temperature and rainfall conditions, millet's significance is unparalleled.

7. AUTHORS' CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agreed to be accountable for all aspects of the work. All the authors are eligible to be an author as per the International Committee of Medical Journal Editors (ICMJE) requirements/guidelines.

8. FUNDING

There is no funding to report.

9. CONFLICTS OF INTEREST

The authors report no financial or any other conflicts of interest in this work.

10. ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

11. DATA AVAILABILITY

All the data is available with the authors and shall be provided upon request.

12. PUBLISHER'S NOTE

13. USE OF ARTIFICIAL INTELLIGENCE (AI)-ASSISTED TECHNOLOGY

The authors declare that they have not used artificial intelligence (AI)-tools for writing and editing of the manuscript, and no images were manipulated using AI.

REFERENCES

1. Kothari SL, Kumar S, Vishnoi RK, Kothari A, Watanabe KN. Applications of biotechnology for improvement of millet crops: Review of progress and future prospects. Plant Biotechnol. 2005;22:81-8. https://doi.org/10.5511/plantbiotechnology.22.81
2. Banerjee P, Maitra S. The role of small millets as functional food to combat malnutrition in developing countries. Indian J Nat Sci. 2020;10:20412-7. https://doi.org/10.1073/pnas.0402892101
3. Sher A, Nawaz A, Sarfraz M, Ijaz M, Ul-Allah S, Sattar A, *et al*. Advanced production technologies of millets. In: Agronomic Crops. Production Technologies. Vol. 1. Berlin: Springer; 2019. p. 273-96. https://doi.org/10.1007/978-981-32-9151-5_15
4. Sharma N, Sharma L, Onkarappa D, Yogendra K, Bose J, Sharma RA. Molecular basis and engineering strategies for transcription factor-mediated reproductive-stage heat tolerance in crop plants. Agronomy. 2024;14(1):159. https://doi.org/10.3390/agronomy14010159
5. Maitra S, Praharaj S, Hossain A, Patro TSSK, Pramanick B, Shankar T, *et al*. Small millets: The next-generation smart crops in the modern era of climate change. In: Omics of Climate Resilient Small Millets. Singapore: Springer Nature Singapore; 2022. p. 1-25. https://doi.org/10.1007/978-981-19-3907-5_1
6. Maharajan T, Ceasar SA, Ajeesh Krishna TP. Harnessing the transcriptomic resources of millets to decipher climate resilience and nutrient enrichment traits. Crit Rev Plant Sci. 2024;43:348-75. https://doi.org/10.1080/07352689.2024.2354981
7. Raut D, Sudeepthi B, Gawande KN, Reddy G, Vamsi S, Padhan SR, *et al*. Millet's role as a climate resilient staple for future food security: A review. Int J Environ Climate Change. 2023;13(11):4542-52. https://doi.org/10.9734/ijecc/2023/v13i113634
8. Kudapa H, Barmukh R, Vemuri H, Gorthy S, Pinnamaneni R, Vetriventhan M, *et al*. Genetic and genomic interventions in crop biofortification: Examples in millets. Front Plant Sci. 2023;14:1123655. https://doi.org/10.3389/fpls.2023.1123655
9. Ghatak A, Pierides I, Singh RK, Srivastava RK, Varshney RK, Prasad M, *et al*. Millets for a sustainable future. J Exp Bot. 2025;76(6):1534-45. https://doi.org/10.1093/jxb/erae507
10. Wilson MKL, VanBuren R. Leveraging millets for developing climate resilient agriculture. Curr Opin Biotechnol. 2022;75:02683. https://doi.org/10.1016/j.copbio.2022.102683
11. Tripathi T, Vyas S. From ancient grains to modern solutions: A history of millets and their significance in agriculture and food security. Int J Home Sci. 2023;9:72-8. https://doi.org/10.22271/23957476.2023.v9.i2b.1466
12. Lim TK. *Coix lacryma-jobi*. In: Edible Medicinal and Non-Medicinal Plants. Berlin: Springer Netherlands; 2012. https://doi.org/10.1007/978-94-007-5653-3_14
13. Osundinakin M, Ogunkanmi A, Onuminya T, Rotimi T, Ogundipe O. Physio-chemical properties responses of six fonio genotypes (*Digitaria exilis* and *D. iburua*) subjected to drought stress conditions. Adv Res Life Sci. 2023;7:22-32. https://doi.org/10.2478/arls-2023-0003
14. Jideani IA. *Digitaria exilis* (acha/fonio), *Digitaria iburua* (iburu/fonio) and *Eleusine coracana* (tamba/finger millet) Non-conventional cereal grains with potentials. Sci Res Essays. 2012;7:3834-43. https://doi.org/10.5897/SRE12.416
15. Tripathi A, Shukla S. Methods of genetic transformation: Major emphasis to crop plants. J Microbiol Biotechnol Food Sci. 2024;13(4):e10276. https://doi.org/10.55251/jmbfs.10276
16. Jaiswal S, Antala TJ, Mandavia MK, Chopra M, Jasrotia RS, Tomar RS, *et al*. Transcriptomic signature of drought response in pearl millet (*Pennisetum glaucum* (L.) and development of web-genomic resources. Sci Rep. 2018;8:3382. https://doi.org/10.1038/s41598-018-21560-1
17. Xing G, Jin M, Qu R, Zhang J, Han Y, Han Y, *et al*. Genome-wide investigation of histone acetyltransferase gene family and its responses to biotic and abiotic stress in foxtail millet (*Setaria italica* [L.] P. Beauv). BMC Plant Biol. 2022;22:292. https://doi.org/10.1186/s12870-022-03676-9
18. Kothai N. Evaluation of salinity stress effects on seed germination and seedling growth and estimation of protein contents in Kodo millet (*Paspalum scrobiculatum* L.). J Stress Physiol Biochem. 2020;16:70-81.
19. Pan J, Li Z, Dai S, Ding H, Wang Q, Li X, *et al*. Integrative analyses of transcriptomics and metabolomics upon seed germination of foxtail millet in response to salinity. Sci Rep. 2020;10:13660. https://doi.org/10.1038/s41598-020-70520-1
20. Bani Hani N, Aukour FJ, Al-Qinna MI. Investigating the pearl millet (*Pennisetum glaucum*) as a climate-smart drought-tolerant crop under Jordanian arid environments. Sustainability. 2022;14:12249. https://doi.org/10.3390/su141912249
21. Magallon WN, Cabahug AG. Field performance of adlai (*Coix lacryma-jobi* L.) under organic planting system in acidic marginal upland in the Philippines. Int J Agric Technol. 2022;18:1671-82.
22. Sedithippa Janarthanan B. Saving farm subsidies with smart climate interventions: The case of transition to a millet-based agriculture. China Agric Econ Rev. 2024;16(2):249-66. https://doi.org/10.1108/CAER-05-2023-0129
23. Zimba S, Dougill A, Chanza C, Boesch C, Kepinski S. Gender differential in choices of crop variety traits and climate-smart cropping systems: Insights from sorghum and millet farmers in drought-prone areas of Malawi. Plants People Planet. 2023;7:689-703. https://doi.org/10.1002/ppp3.10467
24. Naresh RK, Bhatt R, Singh PK, Kumar Y, Tiwari H, Saini A, *et al*. Millet: The super food in context of climate change for combating food and water security: A review. Pharma Innov J. 2023;12(3):1040-9.
25. Prasad PVV, Djanaguiraman M, Stewart ZP, Ciampitti IA. Agroclimatology of maize, sorghum, and pearl millet. In: Agroclimatology: Linking Agriculture to Climate. Vol. 60. Washington, DC: American Society of Agronomy; 2020. p. 201-41. https://doi.org/10.2134/agronmonogr60.2016.0005
26. Mukami A, Ngetich A, Mweu C, Oduor RO, Muthangya M, Mbinda WM. Differential characterization of physiological and biochemical responses during drought stress in finger millet varieties. Physiol Mol Biol Plants. 2019;25(4):837-46. https://doi.org/10.1007/s12298-019-00679-z
27. Terfa GN, Pan W, Hu L, Hao J, Zhao Q, Jia Y, *et al*. Mechanisms of salt and drought stress responses in foxtail millet. Plants (Basel). 2025;14(8):1215. https://doi.org/10.3390/plants14081215
28. Seghatoleslami MJ, Kafi M, Majidi E. Effect of drought stress at different growth stages on yield and water use efficiency of five proso millet (*Panicum miliaceum* L.) genotypes. Pak J Bot. 2008;40(4):1427-32. https://doi.org/10.5455/FAA.277118
29. Bidinger FR, Mahalakshmi V, Rao GDP. Assessment of drought resistance in pearl millet (*Pennisetum americanum* (L.) Leeke). II. Estimation of genotype response to stress. Aust J Agric Res. 1987;38(1):49-59. https://doi.org/10.1071/AR9870049
30. Kholova J, Hash CT, Kumar PL, Yadav RS, Kočová M, Vadez V. Terminal drought-tolerant pearl millet [*Pennisetum glaucum* (L.) R. Br.] have high leaf ABA and limit transpiration at high vapour pressure deficit. J Exp Bot. 2010;61(5):1431-40. https://doi.org/10.1093/jxb/erq013
31. Roy T, Kalambukattu JG, Sarkar A, Rashmi I, Pal R, Singhal V, *et al*. Climate crisis and adoption of climate-smart agriculture technologies. In: Climate Crisis: Adaptive Approaches and Sustainability. Cham: Springer Nature Switzerland; 2024. p. 229-52. https://doi.org/10.1007/978-3-031-44397-8_13
32. Mehta D, Vyas S, Dudhagara D, Patel A, Parmar V. Significance of Indian millets in enhancing global food security: A comprehensive review. Trends Food Sci Technol. 2024;2024:104527. https://doi.

org/10.1016/j.tifs.2024.104527

33. MOAFW (Ministry of Agriculture & Farmers Welfare). Measures to Promote Crop Diversification; 2022. Available from: https://pib.gov.in/pressreleasepage.aspx?prid=1810902#:~:text=the%20department%20of%20agriculture%20%26%20farmers,water%20intensive%20paddy%20crop%20to [Last accessed on 2026 Jan 17].
34. Kumar S, Palve A, Joshi C, Srivastava RK. Crop biofortification for iron (Fe), zinc (Zn) and vitamin A with transgenic approaches. Heliyon. 2019;5(6):e01914. https://doi.org/10.1016/j.heliyon.2019.e01914
35. Khangar NS, Mohanasundari T. Measuring the Environmental Impact of Maize, *Sorghum*, and Millets Production in Madhya Pradesh: A Comparative Analysis Using Life Cycle Assessment. In: Asia Conference on Environment and Sustainable Development. Singapore: Springer Nature Singapore; 2023. p. 151-63. https://doi.org/10.1007/978-981-97-3320-0_12
36. Patil PK, Sathyamoorthy NK, Geethalakshmi V, Manivannan V, Boomiraj K, Kokilavani S. Sustainable pearl millet cultivation: Choices in a changing climate. Maydica. 2024;67(2):101946. https://doi.org/10.1016/j.jafr.2025.101946
37. Cavers PB, Kane M. The biology of Canadian weeds: 155. *Panicum miliaceum* L. Can J Plant Sci. 2016;96(6):939-88. https://doi.org/10.1139/cjps-2015-0152
38. Ancharaz VD, Sultan RA. Aid for Trade and Climate Change Financing Mechanisms. ICTSD; 2010. Available from: https://www.iadb.org/intal/intalcdi/PE/2010/04946.pdf [Last accessed on 2026 Jan 17].
39. Singh S, Suri S, Singh R. Potential and unrealized future possibilities of browntop millet in the food sector. Front Sustain Food Syst. 2022;6:974126. https://doi.org/10.3389/fsufs.2022.974126
40. Zeng Y, Yang J, Chen J, Pu X, Li X, Yang X, *et al*. Actional mechanisms of active ingredients in functional food Adlay for human health. Molecules. 2022;27:4808. https://doi.org/10.3390/molecules27154808
41. Borkar VS, Chordiya MA. Ethno medicinal properties of *Echinochloa colona* and *Hydrolea zeylanica*: A review. World J Pharm Res. 2016;5:354-60.
42. Amare E, Grigoletto L, Corich V, Giacomini A, Lante A. Fatty acid profile, lipid quality and squalene content of teff (*Eragrostis teff* (Zucc.) trotter) and amaranth (*Amaranthus caudatus* L.) varieties from Ethiopia. Appl Sci. 2021;11:3590. https://doi.org/10.3390/app11083590
43. Nani A, Belarbi M, Ksouri-Megdiche W, Abdoul-Azize S, Benammar C, Ghiringhelli F, *et al*. Effects of polyphenols and lipids from *Pennisetum glaucum* grains on T-cell activation: modulation of Ca2+ and ERK1/ERK2 signaling. BMC Complement Alternat Med. 2015;15:426. https://doi.org/10.1186/s12906-015-0946-3
44. Gong Z, Dong L, Lam S, Zhang D, Zong Y, Hao X, *et al*. Nutritional quality in response to elevated CO_2 concentration in foxtail millet (*Setaria italica*). J Cereal Sci. 2021;102:103318. https://doi.org/10.1016/j.jcs.2021.103318
45. Muguerza M, Gondo T, Ishigaki G, Akashi R. Lignin content and digestibility in transgenic bahiagrass (*Paspalum notatum* Flügge) obtained by genetic manipulation of cinnamyl alcohol dehydrogenase gene. Asian J Plant Sci. 2013;13:8-17. https://doi.org/10.3923/ajps.2014.8.17
46. Liu Y, Ren J, Hu Y, Wang S, Mao J, Xu Y, *et al*. Effects of drought stress during the flowering period on the rhizosphere fungal diversity of broomcorn millet (*Panicum miliaceum* L.). Agronomy. 2023;13:2896. https://doi.org/10.3390/agronomy13122896
47. Wasana RKR, Nuwan VGSI, Ediriweera ERHSS. Medicinal and Nutritional Value of *Panicum miliaceum* L. (Meneri): A Review. In: National Research Symposium; 2016.
48. Kumar A, Anju T, Kumar S, Chhapekar SS, Sreedharan S, Singh S, *et al*. Integrating omics and gene editing tools for rapid improvement of traditional food plants for diversified and sustainable food security. Int J Mol Sci. 2021;22(15):8093. https://doi.org/10.3390/ijms22158093
49. Dosad S, Chawla HS. *In vitro* plant regeneration and transformation studies in millets: Current status and future prospects. Indian J Plant Physiol. 2016;21(3):239-54. https:///doi.org/10.1007/s40502-016-0240-5
50. Kothari SL, Agarwal K, Kumar S. Inorganic nutrient manipulation for highly improved in vitro plant regeneration in finger millet-*Eleusine coracana* (L.) Gaertn. *In Vitro* Cell Dev Biol Plant. 2004;40(5):515-9. https://doi.org/10.1079/ivp2004564
51. Mathew SA. *In-vitro* regeneration of Finger millet: Current status and future prospects. Plant Cell Tissue Organ Cult. 2025;160(2):32. https://doi.org/10.1007/s11240-025-02974-y
52. Ragavendran C, Natarajan D. Role of plant tissue culture for improving the food security in India: A review update. In: Sustainable Agriculture Towards Food Security. Berlin: Springer; 2017. p. 231-62. https://doi.org/10.1007/978-981-10-6647-4_13
53. Dosad S, Chawla HS. *In vitro* plant regeneration and transformation studies in millets: Current status and future prospects. Indian J Plant Physiol. 2016;21(3):239-54. https:///doi.org/10.1007/s40502-016-0240-5
54. Olatunji D, Geelen D, Verstraeten I. Control of endogenous auxin levels in plant root development. Int J Mol Sci. 207;18(12):2587. https://doi.org/10.3390/ijms18122587
55. Ssebunya B, Kadzere I, Speiser B, Weidmann G. Pest and disease management in selected organic crops-a resource manual for trainers. 2023. https://doi.org/10.5281/zenodo.7993450
56. Rangan TS. Growth and plantlet regeneration in tissue cultures of some Indian millets: *Paspalum scrobiculatum* L., *Eleusine coracana* Gaertn. and *Pennisetum typhoideum*Pers. Zeitschrift Pflanzenphysiol. 1976;78(3):208-16. https://doi.org/10.1016/S0044-328X(73)80003-0
57. Wakizuka T, Yamaguchi T. The induction of enlarged apical domes *in vitro* and multi-shoot formation from finger millet (*Eleusine coracana*). Ann Bot. 1987;60(3):331-6. https://doi.org/10.1093/oxfordjournals.aob.a087452
58. Kumar S, Agarwal K, Kothari SL. *In vitro* induction and enlargement of apical domes and formation of multiple shoots in finger millet, *Eleusine coracana* (L.) Gaertn and crowfoot grass, *Eleusine indica* (L.) Gaertn. Curr Sci. 2001;81:1482-5.
59. Jamra G, Shah P, Agarwal A, Sharma D, Kumar A. Endogenous phytonutrient, phytochemical, and phytohormone levels modulate *in-vitro* callus induction and plant regeneration in finger millet (*Eleusine coracana*) genotypes. Plant Biosyst Int J Deal Aspects Plant Biol. 2021;156:1-17. https://doi.org/10.1080/11263504.2021.1918779
60. Bernardo EL, Fernandez PG, Aspuria ET, Cadiz NM, Marcelino RT. *In vitro* seedling growth of adlay (*Coix lacryma-jobi* L.) 'Pulot' and its response to 2,4-dichlorophenoxyacetic acid, benzylaminopurine, plain cow dung ash and Agnihotra ash. Philippine Agric Sci. 2020;103:245-55. https://doi.org/10.62550/FK21059017
61. Li G, Cao B, Feng J, Liu W, Yin Y. Pollen morphology, *in vitr*o germination and another culture of *Coix lacryma-job*i L cultivars. SM J Med Plant Stud. 2021;2:784612. https://doi.org/10.36876/smjmps784612
62. Ntui VO, Uyoh EA, Nakamura I, Mii M. Agrobacterium-mediated genetic transformation of Fonio (*Digitaria exilis* (L.) Stapf). Afr J Biotechnol. 2017;16(23):1302-7. https://doi.org/10.5897/AJB2017.15903
63. Dosad S, Chawla HS. Optimization of different doses of growth regulators for *in vitro* regeneration of *Echinochloa frumentacea* Roxb. from caryopsis. Indian J Plant Physiol. 2015;20:339-44. https://doi.org/10.1007/s40502-015-0184-1
64. Yemets AI, Bayer GY, Blume YB. An effective procedure for *in vitro*

culture of *Eleusine coracana* (L.) and its application. Int Scholar Res Notices. 2013;2013:7. https://doi.org/10.1155/2013/853121

65. Dosad S, Chawla HS. *In vitro* plant regeneration from mature seeds of finger millet (*Eleusine coracana*) through somatic embryogenesis. Indian J Plant Physiol. 205;20:360-7. https://doi.org/10.1007/s40502-015-0191-2
66. Pande A, Dosad S, Chawla HS, Arora S. *In-vitro* organogenesis and plant regeneration from seed-derived callus cultures of finger millet (*Eleusine coracana*). Braz J Bot. 205;38:19-23. https://doi.org/10.1007/s40415-014-0102-1
67. Satish L, Ceasar SA, Shilpha J, Rency AS, Rathinapriya P, Ramesh M. Direct plant regeneration from *in vitro*-derived shoot apical meristems of finger millet (*Eleusine coracana* (L.) Gaertn.). *In Vitro* Cell Dev Biol Plant. 2015;51:192-200. https://doi.org/10.1007/s11627-015-9672-2
68. Anju C, Rabindran R, Velazhahan R, Ravikesavan R. Callusing and regeneration in finger millet [*Eleusine coracana* (L.) Gaertn.]. Res J Agric Sci. 2016;7:324-9.
69. Satish L, Rency AS, Rathinapriya P, Ceasar SA, Pandian S, Rameshkumar R, *et al*. Influence of plant growth regulators and spermidine on somatic embryogenesis and plant regeneration in four Indian genotypes of finger millet (*Eleusine coracana* (L.) Gaertn). Plant Cell Tissue Organ Cult. 2016;124:15-31. https://doi.org/10.1007/s11240-015-0870-8
70. Alex N, Cecilia M, Mathew N, Asunta M, Henry O, Wilton M. Efficient plant regeneration protocol for finger millet [*Eleusine coracana* (L.) Gaertn.] via somatic embryogenesis. Afr J Biotechnol. 2018;17:660-7. https://doi.org/10.5897/ajb2018.16452
71. Kashyap A, Penak SM, Saha A, Singh BR. *In vitro* plant development of *Eleusine coracana* via indirect organogenesis and somatic embryogenesis using mature seeds as explants. Curr Sci. 2018;115(1):91-8. https://doi.org/10.5897/AJB2018.16452
72. Kumar S. High frequency *in vitro* plant regeneration from immature inflorescence (from) in finger millet (*Eleusine coracana* (L.) gaertn. J Phytol Res. 2018;31.
73. Mukami A, Ngetich A, Mweu C, Muthangya M, Oduor RO, Ngugi M, *et al*. Rapid and efficient plant regeneration from shoot apical meristems of finger millet [*Eleusine coracana* (L.) Gaertn.] via direct organogenesis. Afr J Biotechnol. 2018;17(29):898-905. https://doi.org/10.5897/AJB2018.16562
74. Feyissa T, Gebremedhen H. Somatic embryogenesis of *Eleusine coracana* on inducted seed explants. Cell Biol Dev. 2021;5(1):26-31. https://doi.org/10.13057/CELLBIOLDEV/V050104
75. Kansara RV, Solanki VH, Srivashtav VS, Patel RM, Gandhi KD, Mehta VS. *In vitro* regeneration through indirect organogenesis, genetic uniformity analysis and mineral content determination of finger millet (*Eleusine coracana* L.). Biologia. 2023;78(1):67-77. https://doi.org/10.1007/s11756-022-01179-4
76. Plaza S, Blösch R, Tadele Z. Efficiency of in vitro regeneration is dependent on the genotype and size of explant in tef [*Eragrostis tef* (Zucc.) Trotter]. Adv Crop Sci Technol. 2015;3(3):1000179. https://doi.org/10.4172/2329-8863.1000179
77. Lee SH, Lee DG, Ki-Won L. Evaluation of forage production and tissue culture efficiency of two teff grass (*Eragrostis teff*) cultivars. Res J Biotech. 2015;10:43-7. https://doi.org/10.5333/KGFS.2019.39.3.185
78. Sang-Hoon L, Dong-Gi L, Ki-Won L. Evaluation of forage production and tissue culture efficiency of two teff grass *(Eragrostis teff*) cultivars. Res J Biotechnol. 2015;10:43-7.
79. Rakhimzhanova AO, Bekkuzhina SS, Zhumabek AT, Ramankulov YM, Manabayeva SA. *In vitro* culture of foreign and local *Panicum virgatum* and *Panicum miliaceum* cultivars. Eur J Appl Biotechnol. 2018;3.
80. Liu B, Wu H, Yang S, Wu E, Yang P, Gao X. Efficient callus induction and regeneration in proso millet. Agron J. 2021;113:4003-12. https://doi.org/10.1002/agj2.20796
81. Chen L, Guan L, Anami E, Adachi T. Establishment of embryogenic suspension culture derived from leaflets of sexual bahiagrass (*Paspalum notatum*) with regeneration ability in long term. Plant Biotechnol. 20011;18(3):209-14. https://doi.org/10.5511/plantbiotechnology.18.209
82. Ye XQ, She JM, Jia XP, Deng YM, Liang LJ, Tong HY, *et al*. Screening technique of salt-tolerant somatic mutant in *Paspalum notatum* Flugge. Jiangsu Nongye Xuebao. 2012;28(6):1247-52.
83. Kothari-Chajer A, Sharma M, Kachhwaha S, Kothari SL. Micronutrient optimization results into highly improved *in vitro* plant regeneration in kodo (*Paspalum scrobiculatum* L.) and finger (*Eleusine coracana* (L.) Gaertn.) millets. Plant Cell Tissue Organ Cult. 2008;94:105-12. https://doi.org/10.1007/s11240-008-9392-y
84. Lakshmi TR, Naji M, Al Ghazali M, Nazir M. Micropropagation and attempts to develop RAPD molecular markers for salt tolerant cultivars of pearl millet. Int J Res Sci. 2015;1(2):33-6. http://dx.doi.org/10.24178/ijrs.2015.1.2.33
85. Maity PJ, Kulkarni VM, Vishnu B. Thidiazuron-induced multiple shoot regeneration and *in vitro* flowering in *Pennisetum glaucum* (L.) R. Br. Phytomorphology. 2016;66(1/2):45-50.
86. Khan RT, Ilyas R, Saleem S, Bibi S, Khan MR, Younas MT, *et al*. Effects of different hormonal concentrations on *in vitro* regeneration and multiplication of pearl millet (*Pennisetum glaucum* L.). J Appl Res Plant Sci. 2022;3:311-6. https://doi.org/10.38211/joarps.2022.3.2.38
87. Fan YH, Xu Y, Zhu SC, Wang JJ, Jia JY, Huang LK. Construction of tissue culture regeneration system of *Pennisetum glaucum*. Acta Agrestia Sin. 2023;31(1):89.
88. Satish L, Rathinapriya P, Ceasar SA, Rency AS, Pandian S, Rameshkumar R, *et al*. Effects of cefotaxime, amino acids and carbon source on somatic embryogenesis and plant regeneration in four Indian genotypes of foxtail millet (*Setaria italica* L.). *In Vitro* Cell Dev Biol Plant. 2015;52:140-53. https://doi.org/10.1007/s11627-015-9724-7
89. Iriawati I, Puspita M, Rodiansyah A. *In vitro* regeneration of foxtail millet (*Setaria italica* (L.) Beauv.) cv. Buru Hotong. J Math Fundam Sci. 2017;49:171. https://doi.org/10.5614/j.math.fund.sci.2017.49.2.6
90. Rathinapriya P, Satish L, Rameshkumar R, Pandian S, Rency AS, Ramesh M. Role of activated charcoal and amino acids in developing an efficient regeneration system for foxtail millet (*Setaria italica* (L.) Beauv.) using leaf base segments. Physiol Mol Biol Plants. 2018;25:533-48. https://doi.org/10.1007/s12298-018-0619-z
91. Santos CM, Romeiro D, Silva JP, Basso MF, Molinari HBC, Centeno DC. An improved protocol for efficient transformation and regeneration of *Setaria italica*. Plant Cell Rep. 2020;39:501-10. https://doi.org/10.1007/s00299-019-02505-y
92. Kumar A, Pathak RK, Gupta SM, Gaur VS, Pandey D. Systems biology for smart crops and agricultural innovation: Filling the gaps between genotype and phenotype for complex traits linked with robust agricultural productivity and sustainability. OMICS. 2015;19(10):581-601. https://doi.org/10.1089/omi.2015.0106
93. Ozyigit II, Yucebilgili Kurtoglu K. Particle bombardment technology and its applications in plants. Mol Biol Rep. 2020;47(12):9831-47. https://doi.org/10.1007/s11033-020-06001-5
94. Animasaun DA, Morakinyo JA, Mustapha OT. Assessment of the effects of gamma irradiation on the growth and yield of *Digitaria exilis* [Haller]. J Appl Biosci. 2014;75:6164. https://doi.org/10.4314/jab.v75i1.1
95. Nura S, Adamu AK, Adelanwa MA, Usman IS, Shehu K. Colchicine-induced mutagenesis for improved growth and yield of fonio (*Digitaria exilis*/[Kippist] Stapf.). Bayero J Pure Appl Sci. 2018;10:126. https://doi.org/10.4314/bajopas.v10i2.22

96. Numan M, Serba DD, Ligaba-Osena A. Alternative strategies for multi-stress tolerance and yield improvement in millets. Genes (Basel). 2021;12(5):739. https://doi.org/10.3390/genes12050739
97. Beyene G, Chauhan RD, Villmer J, Husic N, Wang N, Gebre E, *et al*. CRISPR/Cas9-mediated tetra-allelic mutation of the 'Green Revolution'SEMIDWARF-1 (SD-1) gene confers lodging resistance in tef (*Eragrostis tef*). Plant Biotechnol J. 2022;20(9):1716-29.
98. 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. 2014;15:581. https://doi.org/10.1186/1471-2164-15-581
99. Valentine ON, Edak AU, Ikuo N, Masahiro M. *Agrobacterium*-mediated genetic transformation of Fonio (*Digitaria exilis* (L.) Stapf). Afr J Biotechnol. 207;16:1302-7. https://doi.org/10.5897/ajb2017.15903
100. Gupta P, Raghuvanshi S, Tyagi AK. Assessment of the efficiency of various gene promoters via biolistics in leaf and regenerating seed callus of millets, *Eleusine coracana* and *Echinochloa crusgalli*. Plant Biotechnol. 2001;18:275-82. https://doi.org/10.5511/plantbiotechnology.18.275
101. Sharma M, Kothari-Chajer A, Jagga-Chugh S, Kothari SL. Factors influencing *Agrobacterium tumefaciens*-mediated genetic transformation of *Eleusine coracana* (L.) Gaertn. Plant Cell Tissue Organ Cult. 2010;105:93-104. https://doi.org/10.1007/s11240-010-9846-x
102. Ignacimuthu S, Antony Ceasar S. Development of transgenic finger millet (*Eleusine coracana* (L.) Gaertn.) resistant to leaf blast disease. J Biosci. 2012;37:135-47. https://doi.org/10.1007/s12038-011-9178-y
103. Jagga-Chugh S, Kachhwaha S, Sharma M, Kothari-Chajer A, Kothari SL. Optimization of factors influencing microprojectile bombardment-mediated genetic transformation of seed-derived callus and regeneration of transgenic plants in *Eleusine coracana* (L.) Gaertn. Plant Cell Tissue Organ Cult. 2012;109:401-10. https://doi.org/10.1007/s11240-011-0104-7
104. Bayer GY, Yemets AI, Blume YB. Obtaining the transgenic lines of finger millet *Eleusine coracana* (L.). with dinitroaniline resistance. Cytol Genet. 2014;48:139-44. https://doi.org/10.3103/s0095452714030025
105. Satish L, Ceasar SA, Ramesh M. Improved Agrobacterium-mediated transformation and direct plant regeneration in four cultivars of finger millet (*Eleusine coracana* (L.) Gaertn.). Plant Cell Tissue Organ Cult. 2017;131:547-65. https://doi.org/10.1007/s11240-017-1305-5
106. Pushpa BN, Kurnool K, Shankar AG. Development of finger millet (*Eleusine coracana* (L.) Gaertn.) transgenic for salt tolerance by overexpressing antiporter gene OsSOS1 involved in sodium extrusion. Ind J Pure Appl Biosci. 2020;8(6):598-610. https://doi.org/10.18782/2582-2845.7757
107. Satish L, Rathinapriya P, Muthuramalingam P, Pandian S, Ceasar SA, Ramesh M. Overexpression of *Erianthus arundinaceus* DREB2 transcription factor ameliorates the salinity and drought tolerance in *Eleusine coracana* cultivars. Biol Life Sci Forum. 2020;4(1):8. https://doi.org/10.3390/IECPS2020-08665
108. Gebre E, Gugsa L, Schlüter U, Kunert K. Transformation of tef (*Eragrostis tef*) by *Agrobacterium* through immature embryo regeneration system for inducing semi-dwarfism. South Afr J Bot. 2013;87:9-17. https://doi.org/10.1016/j.sajb.2013.03.004
109. Sandhu S, Altpeter F. Co-integration, co-expression and inheritance of unlinked minimal transgene expression cassettes in an apomictic turf and forage grass (*Paspalum notatum* Flugge). Plant Cell Rep. 2008;27:1755-65. https://doi.org/10.1007/s00299-008-0599-5
110. Bhatt R, Asopa PP, Jain R, Kothari-Chajer A, Kothari SL, Kachhwaha S. Optimization of *Agrobacterium* mediated genetic transformation in *Paspalum scrobiculatum* L. (Kodo Millet). Agronomy. 2021;11:1104. https://doi.org/10.3390/agronomy11061104
111. Jha P, Shashi, Rustagi A, Agnihotri PK, Kulkarni VM, Bhat V. Efficient *Agrobacterium*-mediated transformation of *Pennisetum glaucum* (L.) R. Br. using shoot apices as explant source. Plant Cell Tissue Organ Cult. 2011;107:501-12. https://doi.org/10.1007/s11240-011-0001-0
112. O'Kennedy MM, Crampton BG, Lorito M, Chakauya E, Breese WA, Burger JT, *et al*. Expression of a β-1, 3-glucanase from a biocontrol fungus in transgenic pearl millet. South Afr J Bot. 2011;77(2):335-45. https://doi.org/10.1016/j.sajb.2010.09.016
113. Ramadevi R, Rao KV, Reddy VD. *Agrobacterium tumefaciens*-mediated genetic transformation and production of stable transgenic pearl millet (*Pennisetum glaucum* [L.] R. Br.). *In Vitro* Cell Dev Biol Plant. 2014;50:392-400. https://doi.org/10.1007/s11627-013-9592-y
114. Kouakou T, Kouassi AB, Oulo NA, Gonedelé Bi S, Dinant M, Ledour L. *In vitro* transformation of pearl millet (*Pennisetum glaucum* (L). R. BR.): Selection of chlorsulfuron-resistant plants and long term expression of the gus gene under the control of the emu promoter. Afr J Biotechnol. 2015;14:3112-23. https://doi.org/10.5897/ajb2015.14983
115. Wang MZ. Culturing of immature inflorescences and *Agrobacterium*-mediated transformation of foxtail millet (*Setaria italica*). Afr J Biotechnol. 2011;10:16466-79. https://doi.org/10.5897/ajb10.2330
116. Sood P, Singh RK, Prasad M. An efficient *Agrobacterium*-mediated genetic transformation method for foxtail millet (*Setaria italica* L.). Plant Cell Rep. 2020;39:511-25. https://doi.org/10.1007/s00299-019-02507-w
117. Sine B, Ndiaye A, Kanfany G, Grondin A, Ndiaye A, Faye A, *et al*. Physiological and molecular bases of drought and heat tolerance in pearl millet. In: Pearl Millet in the 21st Century: Food-Nutrition-Climate Resilience-Improved Livelihoods. Singapore: Springer Nature Singapore; 2024. p. 247-78. https://doi.org/10.1007/978-981-99-5890-0_10
118. Nair VD, Devi R. Breeding finger millet for abiotic stress tolerance: Strategies and challenges. In: Genetic Improvement of Small Millets. Singapore: Springer Nature Singapore; 2024. p. 225-77. https://doi.org/10.1007/978-981-99-7232-6_11
119. Wu C, Zhang M, Liang Y, Zhang L, Diao X. Salt stress responses in foxtail millet: Physiological and molecular regulation. Crop J. 2023;11(4):1011-21. https://doi.org/10.1016/j.cj.2023.06.001
120. Numan M, Khan AL, Asaf S, Salehin M, Beyene G, Tadele Z, *et al*. From traditional breeding to genome editing for boosting productivity of the ancient grain tef [*Eragrostis tef* (Zucc.) Trotter]. Plants (Basel). 2021;10(4):628. https://doi.org/10.3390/plants10040628
121. Chakraborty A, Viswanath A, Malipatil R, Semalaiyappan J, Shah P, Ronanki S, *et al*. Identification of candidate genes regulating drought tolerance in pearl millet. Int J Mol Sci. 2022;23(13):6907. https://doi.org/10.3390/ijms23136907
122. Zhou Y, Feng C, Wang Y, Yun C, Zou X, Cheng N, *et al*. Understanding of plant salt tolerance mechanisms and application to molecular breeding. Int J Mol Sci. 2024;25(20):10940. https://doi.org/10.3390/ijms252010940
123. Sharma A, Agrawal S, Chanu KP, Bopche V, Rattan A, Sharma A, *et al*. Millets: A Climate-Resilient Nutricereals for Mitigating Hidden Hunger and Providing Nutritional Security. In Millets: The Multi-Cereal Paradigm for Food Sustainability. Cham: Springer Nature Switzerland; 2024. p. 43-56. https://doi.org/10.1007/978-3-031-64237-1_3
124. Saha D, Gowda MC, Arya L, Verma M, Bansal KC. Genetic and genomic resources of small millets. Crit Rev Plant Sci. 2016;35(1):56-79. https://doi.org/10.1080/07352689.2016.1147907
125. Ambawat S, Singh S, Meena RC, Satyavathi CT. Biotechnological applications for improvement of the pearl millet crop. In: Pearl Millet. United States: CRC Press; 2020. p. 115-38.
126. Nelson R, Wiesner-Hanks T, Wisser R, Balint-Kurti P. Navigating complexity to breed disease-resistant crops. Nat Rev Genet. 2018;19(1):21-33. https://doi.org/10.1038/nrg.2017.82

127. Maharajan T, Krishna TPA, Krishnakumar NM, Vetriventhan M, Kudapa H, Ceasar SA. Role of genome sequences of major and minor millets in strengthening food and nutritional security for future generations. Agriculture. 2024;14(5):670. https://doi.org/10.3390/agriculture14050670
128. Mattoo R, Suman BM. 15 Genomics and Sustainable Practices to Improve Nutrition of Millets with Changing Climate. United States: CRC Press; 2023.
129. Vellaichamy Gandhimeyyan R, Chockalingam V, Muthurajan R, Raman R. Accelerating gene discovery in climate-resilient and nutrient-rich major and minor millets through genome-wide association studies: Progress and prospects. Plant Breed. 2023;142(4):389-406. https://doi.org/10.1111/pbr.13120
130. Sood S, Kumar A, Babu BK, Gaur VS, Pandey D, Kant L, *et al*. Gene discovery and advances in finger millet [*Eleusine coracana* (L.) Gaertn.] genomics-an important nutri-cereal of future. Front Plant Sci. 2016;7:1634. https://doi.org/10.3389/fpls.2016.01634
131. Shivhare R, Lata C. Exploration of genetic and genomic resources for abiotic and biotic stress tolerance in pearl millet. Front Plant Sci. 2017;7:2069. https://doi.org/10.3389/fpls.2016.02069
132. Kage U, Kumar A, Dhokane D, Karre S, Kushalappa AC. Functional molecular markers for crop improvement. Crit Rev Biotechnol. 2016;36(5):917-30. https://doi.org/10.3109/07388551.2015.1062743
133. Ingle K, Thakur N, Moharil MP, Suprasanna P, Awio B, Narkhede G, *et al*. Current Status and Future 11 Prospects of Molecular Marker Assisted Selection (MAS) in Millets. Boca Raton: CRC Press; 2023.
134. Srivastava RK, Singh RB, Pujarula VL, Bollam S, Pusuluri M, Chellapilla TS, *et al*. Genome-wide association studies and genomic selection in pearl millet: Advances and prospects. Front Genet. 2020;10:1389. https://doi.org/10.3389/fgene.2019.01389
135. Ramesh D, Singh S, Shah P, Chakraborty A, Satyavathi TC, Thirunavukkarasu N. Trait mapping, marker-assisted selection, and introgression breeding in pearl millet. In: Pearl Millet in the 21st Century: Food-Nutrition-Climate Resilience-Improved Livelihoods. Singapore: Springer Nature Singapore; 2024. p. 111-40. https://doi.org/10.1007/978-981-99-5890-0_5
136. Zenda T, Liu S, Dong A, Duan H. Advances in cereal crop genomics for resilience under climate change. Life. 2021;11(6):502. https://doi.org/10.3390/life11060502
137. Ceasar A. Genome-editing in millets: Current knowledge and future perspectives. Mol Biol Rep. 2022;49(1):773-81. https://doi.org/10.1007/s11033-021-06975-w
138. Lin CS, Hsu CT, Yang LH, Lee LY, Fu JY, Cheng QW, *et al*. Application of protoplast technology to CRISPR/Cas9 mutagenesis: From single-cell mutation detection to mutant plant regeneration. Plant Biotechnol J. 2018;16(7):1295-310. https://doi.org/10.1111/pbi.12870
139. Weckwerth W, Ghatak A, Bellaire A, Chaturvedi P, Varshney RK. PANOMICS meets germplasm. Plant Biotechnol J. 2020;18(7):1507-25. https://doi.org/10.1111/pbi.13372
140. Mane RS, Prasad BD, Sahni S, Quaiyum Z, Sharma VK. Biotechnological studies towards improvement of finger millet using multi-omics approaches. Funct Integr Genomics. 2024;24(5):148. https://doi.org/10.1007/s10142-024-01438-4
141. Mushtaq M, Ahmad Dar A, Skalicky M, Tyagi A, Bhagat N, Basu U, *et al*. CRISPR-based genome editing tools: Insights into technological breakthroughs and future challenges. Genes (Basel). 2021;12(6):797. https://doi.org/10.3390/genes12060797
142. Kumar M, Prusty MR, Pandey MK, Singh PK, Bohra A, Guo B, *et al*. Application of CRISPR/Cas9-mediated gene editing for abiotic stress management in crop plants. Front Plant Sci. 2023;14:1157678. https://doi.org/10.3389/fpls.2023.1157678
143. Hao JH, Kang X, Zhang L, Chen J, Wang D, Dong S, *et al*. CRISPR/Cas9-mediated SiEPF2 mutagenesis attenuates drought tolerance and yield in foxtail millet (*Setaria italica*). Plant Cell Environ. 2025;48:6043-46. https://doi.org/10.1111/pce.15597
144. Goron TL, Raizada MN. Genetic diversity and genomic resources available for the small millet crops to accelerate a New Green Revolution. Front Plant Sci. 2015;6:157. https://doi.org/10.3389/fpls.2015.00157
145. Shahzad R, Jamil S, Ahmad S, Nisar A, Khan S, Amina Z, *et al*. Biofortification of cereals and pulses using new breeding techniques: Current and future perspectives. Front Nutr. 2021;8:721728. https://doi.org/10.3389/fnut.2021.721728
146. Sood P, Singh RK, Prasad M. Millets genetic engineering: The progress made and prospects for the future. Plant Cell Tissue Organ Cult. 2019;137:421-39. https://doi.org/10.1007/s11240-019-01587-6
147. Kadapa S, Gunturi A, Gundreddy R, Kalwala SR, Mogallapu UB. Agronomic biofortification of millets: New way to alleviate malnutrition. In: Millets-Rediscover Ancient Grains. London: IntechOpen; 2023. https://doi.org/10.5772/intechopen.110805
148. Rao CK, Annadana S. Nutrient Biofortification of Staple Food Crops: Technologies, Products and Prospects. Phytonutritional Improvement of Crops. United States: John Wiley & Sons Ltd.; 2017. p. 113-83. https://doi.org/10.1002/9781119079972.ch3
149. Ofori KF, Antoniello S, English MM, Aryee AN. Improving nutrition through biofortification-A systematic review. Front Nutr. 2022;9:1043655. https://doi.org/10.3389/fnut.2022.1043655
150. Govindaraj M, Karthikeyan A, Shobhana VG, Warkentin TD. Genomics-integrated breeding for carotenoids and folates in staple cereal grains to reduce malnutrition. Front Genet. 2020;11:44. https://doi.org/10.3389/fgene.2020.00414
151. Kiran A, Wakeel A, Mahmood K, Mubaraka R, Hafsa, Haefele SM. Biofortification of staple crops to alleviate human malnutrition: Contributions and potential in developing countries. Agronomy. 2022;12(2):452. https://doi.org/10.3390/agronomy12020452
152. Raina A, Laskar RA, Wani MR, Khan S. Plant breeding strategies for abiotic stress tolerance in cereals. In: Omics Approach to Manage Abiotic Stress in Cereals. Singapore: Springer Nature Singapore; 2022. p. 151-77. https://doi.org/10.1007/978-981-19-0140-9_8
153. Maja MM, Ayano SF. The impact of population growth on natural resources and farmers' capacity to adapt to climate change in low-income countries. Earth Syst Environ. 2021;5(2):271-83. https://doi.org/10.1007/s41748-021-00209-6
154. Srikanth P, Sivakumar D, Sharma A, Kaushik N. Recent developments in omics techniques for improving plant abiotic stress using microbes. Int J Environ Sci Technol. 2024;22:1-24. https://doi.org/10.1007/s13762-024-05957-2
155. Samtani R, Mishra SS, Neogi SB. Millets: Small grains, big impact in climate action. J Climate Change Health. 2024;20:100345. https://doi.org/10.1016/j.joclim.2024.100345
156. Paterson AH, Bowers JE, Bruggmann R, Dubchak I, Grimwood J, Gundlach H, *et al*. The Sorghum bicolor genome and the diversification of grasses. Nature. 2009;457(7229):551-6. https://doi.org/10.1038/nature07723
157. Mace ES, Tai S, Gilding EK, Li Y, Prentis PJ, Bian L, *et al*. Whole-genome sequencing reveals untapped genetic potential in Africa's indigenous cereal crop sorghum. Nat Commun. 2013;4:2320. https://doi.org/10.1038/ncomms3320
158. Varshney RK, Shi C, Thudi M, Mariac C, Wallace J, Qi P, *et al*. Pearl millet genome sequence provides a resource to improve agronomic traits in arid environments. Nat Biotechnol. 2017;35(10):969-76. https://doi.org/10.1038/nbt.3943
159. Sehgal D, Skot L, Singh R, Srivastava RK, Das SP, Taunk J, *et al*. Genomic selection for grain yield and drought-related traits in pearl millet. Plant Genome. 2021;14(1):e20090.

160. Bennetzen JL, Schmutz J, Wang H, Percifield R, Hawkins J, Pontaroli AC, *et al*. Reference genome sequence of the model plant *Setaria italica*. Nat Biotechnol. 2012;30(6):555-61. https://doi.org/10.1038/nbt.2196
161. Mamidi S, Healey A, Huang P, Grimwood J, Jenkins J, Barry K, *et al*. A genome resource for green millet *(Setaria viridi*s) enables discovery of agronomically valuable loci. Nat Biotechnol. 2020;38:1203-10. https://doi.org/10.1038/s41587-020-0681-2
162. Muthamilarasan M, Prasad M. Advances in *Setaria* genomics for genetic improvement of cereals and bioenergy grasses. Theor Appl Genet. 2015;128(1):1-14. https://doi.org/10.1007/s00122-014-2399-3
163. U.S. Department of Agriculture, Foreign Agricultural Service. Millet Explorer: World Production Data. International Production Assessment Division (IPAD); 2025. Available from: https://ipad.fas.usda.gov/cropexplorer/cropview/commodityview.aspx?cropid=0459100 [Last accessed on 2026 Jan 17].

How to cite this article:
Chhajer AK, Gour VS, Kumar P, Raj A, Tayal P, Rathi D, Sahil M, Kothari SL. Biotechnology of millets: Current scenario and future prospects (under agricultural biotechnology for climate-resilient crops). JAppl Biol Biotech 2026. Article in Press. http://doi.org/10.7324/JABB.2026.273153