Chapter

Drought Stress in Millets and Its Response Mechanism

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Abstract

Drought is a major abiotic stress that diminishes crop yield and weakens global food security, especially in the current emerging situation of climate change as well as increases in the prevalence and severity of stress elements. Millets are nutrient-dense and capable to resist variety of harsh environmental conditions, including lack of moisture. Millet's crop has evolved dynamically in terms of morphology, physiology, and biochemically that allow them to flee and/or adapt to adverse environmental situations. Drought stress has a significant impact on the vegetative and reproductive phases of plants. Millets generate a very low yield compared to main cereals like wheat and rice, despite their agronomic, nutritional, and health-related benefits. It is necessary to understand how these complex features are regulated and ameliorated the impact of droughts on millet productivity. Keeping this in view, the present work aims to understand the processes used for reducing the negative impacts of droughts in the production of millets varieties using advanced agronomic management strategies (use of information technology) and the biotechnology (improvements in crop genetics).

Keywords: millets, drought, abiotic stress, morphology, physiology

1. Introduction

Millets are the major cereal crop in the developing world, particularly in Africa and Asia's arid and semi-arid tropical regions, where they are utilised in food both for humans and cattle [1]. Millets also play a key role in the subsistence of people living in the mountains. In addition to addressing the issue of the food security at a global level, efforts need to be directed towards such indigenous crops that could flourish amidst the scenario of water scarcity. It is believed that the changing climate will have significant effects on the types of crops cultivated in the next century. Millets are known for their climate-resilient characteristics, such as their ability to adapt to a wide range of ecological conditions, reduced irrigation requirements, improved growth and productivity under low nutrient input conditions, reduced reliance on synthetic fertilisers, and low vulnerability to environmental stresses. Millets might provide alternative climate-smart crops as their adaptation to challenging environments is better than the current major crops of the world [2].

In line with Asia and Africa's food security, millets contribute to over half of the Africa's entire cereal production, together with sorghum. Millets are thus regarded as a poor man's crop because of their major contributions to the diets of resource-constrained producers and consumers. Millets are the primary source of nutrition for small farmer communities in India, Africa, China, and parts of Central America, and they help to ensure food security in Asia and Africa's low-income countries. Millets are ancient food crops which are highly nutritious and can be grown under marginal environmental conditions. Millets are the major energy source and highly nutritious staple foods for sustenance. Millets, often known as 'miscellaneous or coarse cereals,' are a group of small edible grasses in the Poaceae family. In total, millets are distributed around 10 genera and 20 species [3]. Approximately 31,019,370 tonnes of Millets were produced globally in 2018 [4]. Among the summer crops millet's water requirement is much less than those of the two main crops, viz., wheat and rice. Millets are also known as famine crops because these are the only crops assuring yields in famine conditions. About 80% of the millets are used for food and the rest are stocked as feed. Millets have good grain quality that's why it is used in processing industries. Millets have many nutritional, pharmaceutical and nutraceutical properties. They are especially rich in fibre content and starch. They are used in reducing the risk of diabetes, help to lower the cholesterol and are rich in antioxidant activity [5].

Millets are considered to be the essential crops in world's agricultural system due to their resistance to pests and diseases, short growing season and capable to grow in extreme environmental conditions, and because of moderate productivity under enduring water stress conditions when major cereals cannot be relied upon to provide sustainable yields [6]. Millets will stand up to all unwell effects of temperature change apart from doable higher ozone concentrations around urban zones. However, millets would be least struck by increasing greenhouse gas levels within the native microclimate. Similar to maize and sorghum, millets possess a C4 photosynthesis system, hence they avoid photorespiration. As a result, they efficiently utilise the insufficient moisture present in the semi-arid regions. Since C4 plants are able to close their stomata for long periods, they can considerably reduce moisture loss through the leaves.

2. An overview: small millets

Millets are categorised by a collective term accustomed to see a various group of small-seeded annual C4 Panicoid grasses such as barnyard millet (*Echinochloa frumentacea*), finger millet (*Eleusine coracana*), foxtail (*Setaria italica*), pearl millet (*Pennisetum glaucum* (L.) R. Br.), kodo millet (*Paspalum scrobiculatum* L.), little millet (*Panicum sumatrense* Roth ex Roem. & Schult.) and proso millet (*Panicum miliaceum*) (**Figure 1**) [6]. These are extensively cultivated as food and fodder crops in temperate, sub-tropical and tropical regions across the globe [7, 8] and have outstanding biological process properties. Salient features of the millet's crops are described in **Table 1**.

2.1 Importance of millets crop

Millets can withstand extreme temperatures, droughts, and floods. Millets grow well in arid zones/rain-fed locations with marginal soil fertility and moisture. Because of its effective root system, millets require far less water than other cereal crops for their production. Some crops and their water availability are shown in **Table 2**. Millets are grown with organic inputs and do not require synthetic fertilisers or pesticides.

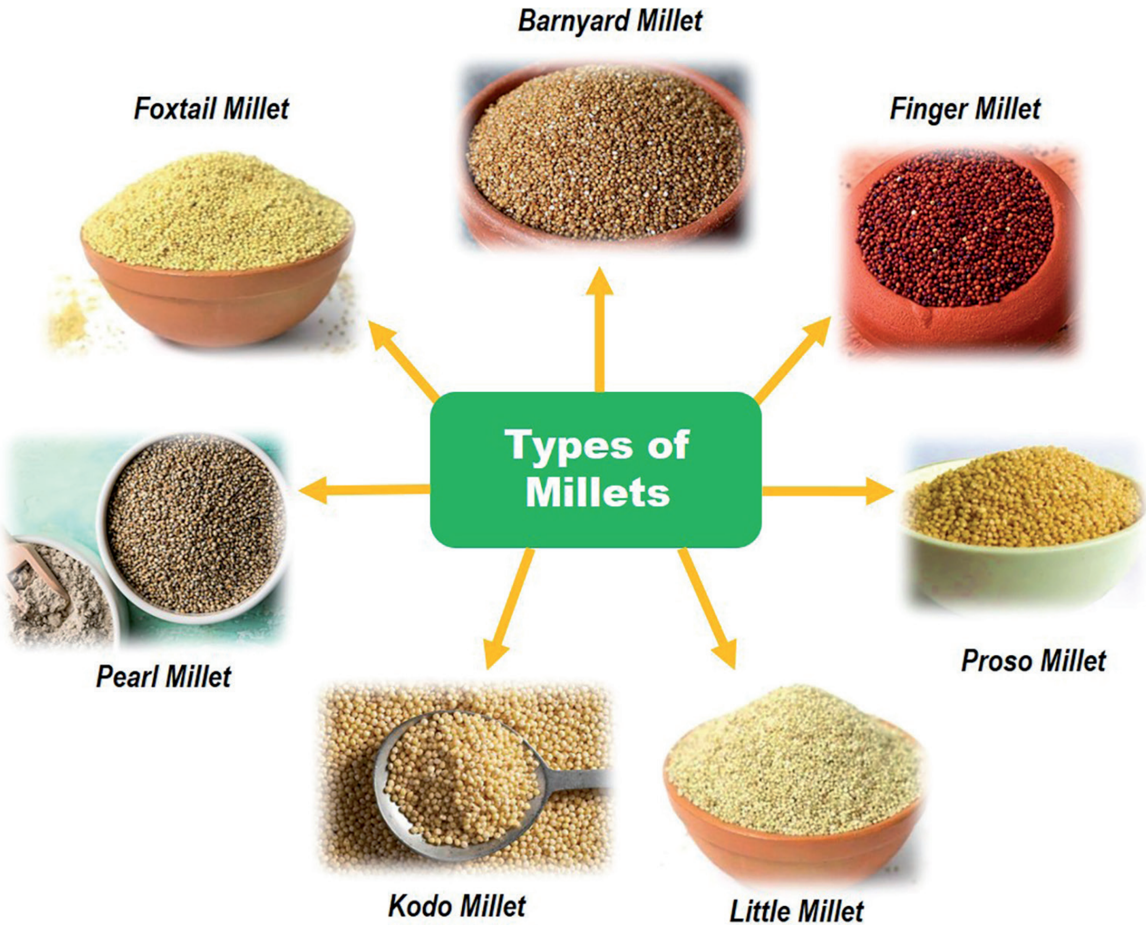

Figure 1.
Representation of different types of small millets grown in the semi-arid regions.

Pesticides are avoided since millets are less susceptible to illnesses and pests. Millets contribute to climate change mitigation by lowering CO_2 levels in the atmosphere [9]. They have a high capacity for carbon sequestration, which aids climate adaptation, particularly in light of global projections of rising methane emissions from rice fields. Millet diets are beneficial for persons with celiac disease and diabetes since they contain no gluten and have a low glycaemic index [1]. Millets crop like pearl millet is most recently used as a low-cost substitute for maize in poultry and animal feed. Millet crops are also used in fermented food and drinks products.

One of the major concerns of the global world is the abrupt changes in the earth's environment, which have had a devastating effect on the earth's ecology

S. No.	Crop Type	Rainfall Requirement (mm y^{-1})
1.	Sugarcane	2000–2200
2.	Banana	2000–2200
3.	Rice	1200–1300
4.	Sorghum	400–500
5.	Bajra	350–400
6.	Ragi	350–400

Table 2.
Rainfall requirement for various crops [7].

Millet Type	Characteristics							
	Vernacular Names	**Botanical Name**	**Family**	**Ploidy level**	**Chromosome no.**	**Use**	**Nutritional values**	**Agronomic benefits**
Barnyard millet	Barnyard millet (English), Madira, Sawa, Kudraivali, a million-dollar grass and oodalu	*Echinochloa frumentacea* L.	Gramineae	Hexaploid	2n = 6× = 36	Food and Feed	Anti-diabetic and high protein content	Early maturity, anti-fungal
Finger millet	Ragi, koda, mandua, nachani or nagli, African birds' foot, rapoko, koracan, kurakkan.	*Eleusine coracana* (L.) Gaertner	Gramineae	Hexaploid	2n = 6× = 36	Food and Feed	Rich in calcium, methionine and tryptophan	Drought and salt tolerance
Pearl millet	Bajra, gero, hegni, sanyo, dukhon and mahangu	*Pennisetum glaucum*	Gramineae	Diploid	2n = 2× = 14	Food, feed	High protein, starch & minerals	Drought & heat tolerance
Foxtail millet	Kangni (Hindi), Navane (Kannada), Thinai (Tamil), Kang (Gujarati) and Rala (Marathi)	*Setaria italica*	Gramineae	Diploid	2n = 2× = 18	Food, biofuel	—	Drought tolerance
Kodo millet	Kodo millet (English), Varagu, Haraka and Arikalu	*Paspalum scrobiculatum*	Gramineae	Tetraploid	2n = 4× = 40	Food and Feed	High-quality protein	Drought tolerance
Little millet	Little millet (English), Sawai, Samalu	*Panicum sumatrense* L.	Gramineae	Tetraploid	2n = 4× = 36	Food	High in phytochemicals, fibre	Abiotic stress tolerance
Proso millet	Proso, Cheena, Panivaragu, Variga and Baragu	*Panicum miliaceum*	Gramineae	Tetraploid	2n = 4× = 36	Food and feed	Rich in amino acids	Drought tolerance, early maturity

Table 1.
Salient features of millets crop [6].

[10]. Currently, we are in the age of an agrarian crisis, which has necessitated for crop improvement to tackle the negative effects of climate change. Intensive agriculture of a few crops for food needs has resulted in poor nutrition and genetic degradation, as well as the negligence of locally nutritious crops. Agriculture is the largest consumer of water in India and in the world. In the Central Himalayan part of India, only about 10% of the cultivated land is under irrigation system. It is largely because the millet crops, unlike rice and wheat, have high water use efficiency and the major chunk of the cultivated land in the summer season is devoted to the millet crops. In contemporary times when water is increasingly becoming scarce, we should conserve and make economical use of water resources at each micro- and meso-scale (farmers' field to watershed scale). The millet crops hold great promise for the strategies of conserving water resources and fight against drought conditions. The millet crops can prove to be helpful in making strategies for conserving water resources and handling drought conditions. Millets are tolerant to the harsh climatic and soil conditions seen in Asia and Africa's semi-arid regions. Millets can be easily grown in harsh environments, particularly in those areas that have insufficient precipitation, low soil fertility, and are unsuitable for the world's primary crops.

Water deficit is one of the most environmental stresses affecting agricultural production and productivity around the world and may result in considerable yield reduction [13]. Hundreds of genes and their products respond to Water stress at transcriptional and translational level [14]. It can be asserted in the context of climate change, millets could be the answer to fighting climate change, poverty and malnutrition. Drought-proofing crops by producing heat-resistant cultivars is one aspect of this adaptation approach for millet crops [11, 12]. In comparison to most of other major crops such as rice and wheat, millets are highly flexible and stress resistant. Water stress affects these millet crops frequently and the problem appears to be becoming worse as weather and climate change is becoming more evident. Millets are agronomically advantageous because they are drought, heat, salt, and biotic stress tolerant, and they may live in marginal lands under rainfed circumstances. Drought-resistance mechanisms in many cereals have been studied by various researchers, but millets drought tolerance has been limited due to a number of factors. The response mechanism of plants in response to drought stress must be assessed. The goal of the present study is to evaluate changes in the millets crop's morphological, physiological, biochemical and molecular features as a result of drought stress, as well as plant tolerance mechanisms to the stress. Elements of drought stress in important millets crops such as finger millet, pearl millet, barnyard millet, foxtail millet, and proso millet were examined in this study. The current methods for discovering drought tolerance genes and metabolic pathways are also discussed. Recent advances in elucidating essential drought stress responses, phenotyping and QTL mapping for drought tolerance, genetic engineering of drought-tolerant crops, and crop management have also been reviewed.

2.2 Drought stress

Drought is outlined as "a temporary reduction in wetness accessibility, in which the amount of available water is significantly below normal for a specified period" and is one of the most common environmental stresses [10]. This condition negatively affects growth and productivity of crops. Water stress is a natural phenomenon in rain-fed (unirrigated) cultivated areas. In general, water stress often causes a series of morphological, physiological, biochemical and molecular changes that unfavourably affect plant growth, development and productivity. Plants are subjected to biotic and abiotic stressors, both of which have a significant impact on their survival [10]. Abiotic stressors are important environmental factors that limit crop productivity and affect the quality and amount of crop yield. Particularly water stress directly affects the physiology of plants, especially photosynthesis. In mountains, summer (*kharif*) crops often encounter water stress. In the face of a global scarcity of water resources, drought has already become a primary factor in limiting crop production worldwide. Water-limited crop production depends on the intensity and the pattern of drought which varies from year to year [15]. The severity of water shortage imposed on field crops also depends on the susceptibility of crops during different stages of their development. The general effects of drought on plant growth are well known. When soil moisture is deficient, crop establishment may be reduced, limited growth of plants, normal development patterns disrupted and eventually, final yield is lowered [16, 17].

2.3 Effects of water stress in millets

Plant cellular activities, growth, development, and economic yield are all affected by water stress. It affects the structure of membranes and organelles at the cellular level, as well as the hydration and structure of proteins and nucleic acids, and the pressure differential across the membrane cell wall complex. Drought causes stomatal closure, which leads to an excessive accumulation of reactive oxygen species (ROS) and oxidative stress. Lipid peroxidation and damage to other biomolecules occur because of this stress [18]. Phytohormones including Abscisic Acid (ABA) and Ethylene (ET) are frequently engaged in drought stress signalling and tolerance. Plant tolerance to drought, salt, and heat stress is improved by salicylic acid (SA) and jasmonic acid (JA) [19]. Plant height, length, biomass, weight, and grain number have all decreased as a result of drought stress in finger millet [20]. Water stress result a decrease in chlorophyll, photosynthesis, and RWC, as well as an increase in proline concentration, in both barnyard and finger millets. Finger millet demonstrated higher levels of tolerance than barnyard millet [21]. Drought-induced oxidative stress caused droopy shoots, curling leaves, increased proline, catalase and malondialdehyde (MDA) content, electrolyte leakage, impaired membrane integrity, and a considerable rise in H_2O_2 in finger and barnyard millets [21]. In finger millet, see [18] found an increased activities of antioxidant enzymes such as glutathione reductase (GR), superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione peroxidase (GPX) and catalase (CAT) during drought stress. A low photosynthetic and stomatal conductance rates, reduced root respiration, accumulation of protective metabolites (serine, threonine, valine, fructose, glucose, maltose, isomaltose, malate, itaconate) in roots, and better utilisation of carbon and nitrogen were found in a high temperature tolerant variety of foxtail millet [22]. The effect of water stress on different millets crop is given in **Table 3**.

To cope with various environmental challenges, plants have evolved various morphological, biochemical, physiological, and molecular systems. Plant cells detect stress events through a variety of sensors, which activate a variety of signalling pathways. Plant hormones, secondary messengers, transcription regulators, and signal transducers are all involved. Drought stress has a variety of effects on plants vegetative growth, reproductive development and molecular level, and are all affected by these changes (**Figure 2**).

Crop	Drought stress	Effect on plant	References
Finger millet	Drought stress was applied in two regimes (fully irrigated and after drought)	Significant reduction in leaf area, dry matter accumulation, seed weight, radiation use efficiency and yield	[21]
Finger millet	Drought stress was applied in two regimes (fully irrigated and after drought)	Results showed that reduction in plants growth, chlorophyll content due to drought stress	[22]
Pearl millet	After 3 weeks of germination drought stress was induced by ceasing water for 4 weeks	They observed a significant reduction in plant height, biomass, panicle, stalk length, no. of leaves, total grain number and weight	[23]
Finger millet and barnyard millet	Water stress was given (control, mild, medium, and severe condition	A significant reduction in chlorophyll content while MDA, proline and CAT activity increased during stress	[24]
Finger millet and barnyard millet	Water stress was given (control, mild, medium, and severe condition	Significant reduction in protein, carbohydrate, amylase and relative water content	[25]
Finger millet	Stress was given to plant by holding irrigation to 45-day old plants	Their results showed droopy, curling leaves, increased amount of proline, MDA, electrolyte leakage, Hydrogen peroxide and antioxidant activities.	[16]
Proso millet	Well- watered, drought stress at vegetative stage, ear emergence stage, seed filling stage and vegetative and seed filling stages	Drought stress results reduction in grain yield, Water use efficiency and harvest index	[26]
Pearl millet and sorghum	Controlled and stressed condition	Results showed that under water stress condition leaf water potential, rates of stomatal conductance, photosynthesis and transpiration decreased more in sorghum than in pearl millet	[27]

Table 3.
Effect of water stress on millets crop.

2.4 Morphological and physiological adaptations to stress in millets

Drought causes distinct morphological and physiological changes in millets crops, which can be seen at various phases of plant growth. Millets have a short life cycle and plant heights, as well as small leaf regions, thickened cell walls, and dense root systems, all of which aid in stress resistance. The morphological response of millets can often be divided into two categories: shoot and root. Changes in leaf form, leaf expansion, leaf area, leaf size, leaf senescence, leaf pubescence, leaf waxiness, cuticle tolerance, and shoot length are all components of the shoot. Changes in root dry weight, root density, and root length are included in the lower root section. Several studies have found that the relationship between morphological and physiological features including grain yield per plant, grain spike per plant, spike fertility, plant height, root length, shoot length, harvest index, chlorophyll content and relative

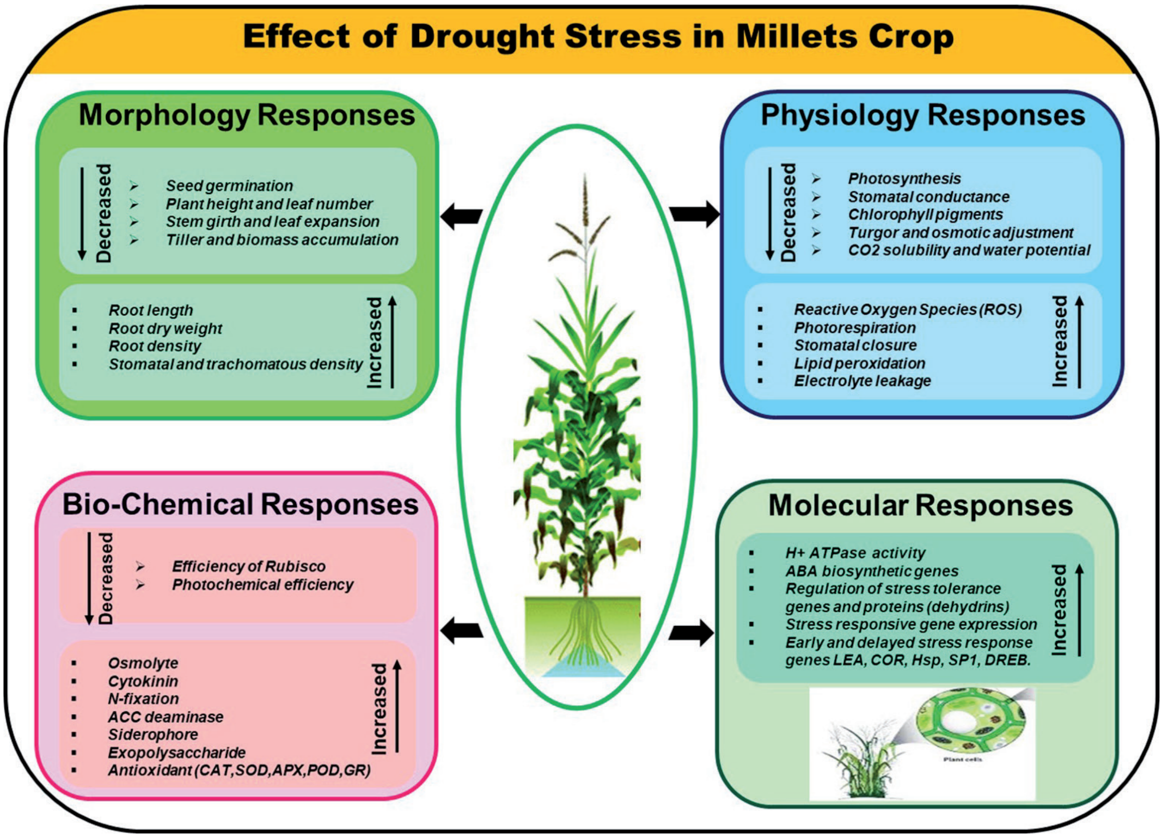

Figure 2.
Effect of drought stress on millets crop and its possible responses.

water content can be used to screen drought-tolerant crops. The various morphological and physiological adaptations of millets to water stresses are summarised in (**Table 4** and **Figure 3**).

2.5 Biochemical adaptations to stress in millets

Drought means water loss and dehydration at normal or even temperatures. Shrinking of cell leads to loss of turgor, osmotic stress and change of membrane potentials, upon severe water loss from the cells, membrane disintegration and abolition of metabolic processes occur [32]. In finger and barnyard millets, the biochemical adaptation response to water stress consists of increased proline content, reduced relative water content, and chlorophyll content [2, 6]. In barnyard and finger millets, some antioxidant enzymes represent adaptive mechanism against water stress. This consists of CAT, phenol and flavonoid content [2]. According to see [33], suggested that during drought stress condition in pearl millet, a higher expression of secondary metabolite genes associated with alkaloid, terpenoid, flavanols, lignin, wax, mevalonic acid (MVA), and Shikimic acid (SA) metabolic pathways were observed in flowering stage than vegetative stage. Following are some stress response mechanisms which takes place in millets during water stress condition (**Table 5** and **Figure 3**).

2.6 Molecular response against water stress in millets

The genome and transcriptome sequences of plants give crucial information for identifying the types of genes involved in the control of drought tolerance, especially in plants that are more resistant to water scarcity. In a study on transcriptome

Crop	Morpho-physiological parameters	Effect on plants	References
Little millet	Root length and shoot length	Root length increased gradually in all drought condition while shoot length decreased	[28]
Foxtail	Root hair density and length	Results showed that under water stressed condition root hair density and length increased.	[29]
Foxtail	Root length and shoot length	A significant reduction in shoot length while root length increased	[30]
Finger millet	Plant height, leaf area total dry matter (TDM), root/shoot ratio by weight and length, grain yield and harvest index	Plant height, leaf area, total dry matter ,root/shoot ratio by weigh, grain yield and harvest index decreased while root/shoot ratio by length increased	[18]
Finger millet and barnyard millet	Relative water content and chlorophyll content	Moderate rate of decline of RWC and chlorophyll	[24, 25]
Proso millet, Foxtail millet and Pearl millet	Seed number per ear and ear number per plant number of tiller, harvest index ear, peduncle and ear length and plant height	Water stress caused reduction in the number of tiller and ear, peduncle and ear length, seed no., harvest index and plant height. Their results showed that foxtail millet showed the greatest yield in both stress and non-stress conditions among other crops.	[31]
Finger millet	Leaf area, dry matter, seed weight and yield	Significant reduction in leaf area, dry matter accumulation, seed weight, radiation use efficiency and yield	[21]
Pearl millet	Plant height, biomass, panicle, stalk length, no. of leaves, total grain no. and weight	They observed a significant redcution in plant height, biomass, panicle, stalk length, no. of leaves, total grain number and weight	[23]

Table 4.
Morphological and physiological adaptations to stress in millets.

sequencing in finger millet provides information of 2824 genes under water stress condition [39]. According to see [40], SiLEA14 gene from foxtail millet, increased the tolerance in transgenic Arabidopsis plants to salt and osmotic stress. The induction of AKR1 gene (Aldo Keto Reductases) in roots and leaves of finger millets is studied with increasing water stress and salt stress. The up-regulated AKR1 gene shows physical defence against oxidative stress (**Table 6** and **Figure 3**).

A single gene known as -carbonic anhydrase (PgCA) was continuously up-regulated in pearl millet exposed to several abiotic stimuli such as drought, salinity, and heat [57]. There are other genes which are known to be involved in drought response or tolerance in millets were EcDehydrin 7 [49], Ec-apx1 [50], EcbHLH57 [51], EcbZIP60 [52], EcGBF3 [53], EcbZIP17 [54], mt1D [55], Metallothionein, Farnesylated protein ATFP6, Farnesyl pyrophosphate synthase and Protein phosphatase 2A, RISBZ4 [56] from finger millet, SiARDP [41], SiCDPK24 [42], SiLTP [43], SiATG8a [44], SiNF-YA1 and SiNFYB8 [45], SiASR1 [46], SiASR4 [47] and SiMYB56

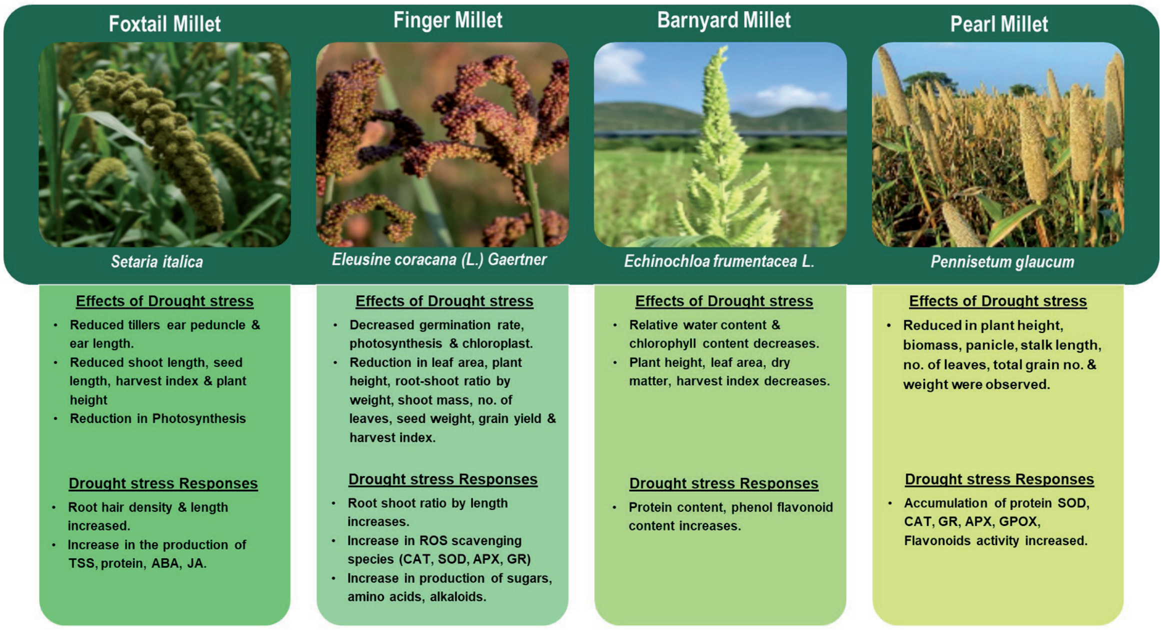

Figure 3.
Effect and response mechanism of drought tolerant millets.

[48] wild foxtail millet and PgGPx [58], PgRab7 [59] and PgeIF4A [60] from wild foxtail millet.

3. Management techniques for water stress in millets

In order to manage water stress, genetic advancements must be combined with appropriate cultural behaviours. To cope water stress, several cultural practices should be done. In recent year, conventional and molecular breeding techniques have been evolved to improve stress tolerance in plants.

3.1 Improvement of water use efficiency in millets

To improve water, use efficiency of millets, multiple factors such as physiological characteristics, time of planting, soil characteristics, meteorological conditions frequency of tillage and application of herbicide, should be measured properly [20, 6].

3.2 Conventional breeding

In conventional breeding, old plant breeding techniques such as introduction, selection and hybridization were used for the identification of stress-tolerant genetic traits in crops [24]. The major phases in conventional breeding are the artificial introduction of water stress and the selection of stress tolerant genotypes. Through hybridization, stress tolerant genes can be transferred into commercially growing types for improved performance under water stress conditions. Drought resistance selection can be done in the field or in a greenhouse. The field environment is particularly ideal for selection work. When it comes to determining which features to utilise to improve selection efficiency, those that contribute to productivity will be more valuable than those that contribute to survival. Using managed field-based stress

Crop	Biochemical parameters	Plants adaptation mechanism	References
Finger millet and barnyard millet	MDA, proline, CAT, phenol and flavonoids	A significant increase in MDA, proline, CAT, phenol and flavonoids activity during stress condition in both the millets crop	[24]
Finger millet and barnyard millet	Protein, carbohydrates and amylase	Significant reduction in protein, carbohydrate and amylase content	[25]
Finger millet	Proline, MDA, electrolyte leakage, Hydrogen peroxide and antioxidant activities.	Significant accumulation of proline, MDA, electrolyte leakage, Hydrogen peroxide and increased antioxidant activities.	[16]
Finger millet	Proline, glycine betaine and TSS and antioxidant enzymes (SOD, CAT, APX, GPX)	Accumulation of Proline, glycine betaine and TSS and antioxidant enzymes (SOD, CAT, APX, GPX) increased under stress.	[34]
Foxtail millet	TSS, proline, ABA and JA phytohormones	Significant increase in TSS, TSS, proline, ABA and JA phytohormones	[35]
Pearl Millet	Proline, superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR), ascorbate peroxidase (APX) and guaiacol peroxidase (GPOX) activities	Accumulation of Proline, superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR), ascorbate peroxidase (APX) and guaiacol peroxidase (GPOX) activities increased	[36]
Pearl Millet	ABA and water potential	Accumulated, higher ABA content while water potential decreased in stress condition	[37]
Pearl millet	Flavonoids, lignin, terpenoids	A higher accumulation of flavonoids, lignin and terpenoids under water stress condition	[38]

Table 5.
Biochemical adaptations to stress in millets.

around the blooming period, when crop is particularly susceptible to water stress has been the key to enhanced pace of advancement in breeding and selection.

3.3 Molecular breeding

Plant genome improvement is insufficient for the development of novel plant varieties using traditional breeding approaches. Since the 1990s, molecular markers have been utilised to identify superior hybrid lines to overcome this barrier in plant breeding procedures. Molecular breeding is evolving a new breeding technology, which has the potential to improve crops dramatically. The majority of attributes including stress tolerance, are quantitative and influenced heavily by the environment. With the help of molecular breeding techniques, many biofortified crops and plant types with high yielding variety with new characteristics like pest and disease resistant were developed. Marker-assisted breeding (known as gene stacking) is a more efficient and cost-effective method than traditional breeding, which makes it impossible to transfer many resistance genes into a single agricultural plant at

Genes	Plants response	References
Foxtail millet		
SiLEA 14	It enhances tolerance in Arabidopsis plants to drought stress	[40]
SiARDP	Increased drought and salt tolerance in transgenic Arabidopsis	[41]
SiCDPK24	Improved drought resistance in transgenic Arabidopsis	[51]
SiLTP	Enhanced drought and salt tolerance in transgenic tobacco	[52]
SiATG8a	It enhances tolerance in Arabidopsis plants to drought stress and nitrogen starvation	[53]
SiNF-YA1, SiNFYB8	Increased drought, salinity and osmotic stress tolerance in tobacco	[54]
SiASR1	Improved tolerance to drought and oxidative stress tolerance in transgenic tobacco	[55]
SiASR4	Increased drought and salt stress tolerance in transgenic foxtail millet and Arabidopsis	[56]
SiMYB56	It enhances drought tolerance in transgenic rice plants	[57]
Finger millet		
EcDehydrin7	Overexpression of EcDehydrin7 increased drought tolerance in transgenic tobacco	[42]
Ec-apx1	Enhanced drought tolerance in plant	[43]
EcbHLH57	Conferred drought, salt and oxidative tolerance in transgenic tobacco plants	[44]
EcbZIP60	Displayed tolerance to drought stress with enhanced photosynthesis in tobacco	[45]
EcGBF3	Enhanced drought, Osmotic and salinity tolerance in Arabidopsis	[46]
EcbZIP17	Improved tolerance to various environmental stresses via ER signalling pathways	[47]
Mt1D	Overexpression of mt1D in finger millet showed better osmotic adjustment and chlorophyll retention under drought	[48]
Metallothionein	Increased drought tolerance	[49]
Farnesylated protein ATFP6	Improved tolerance to drought stress	[49]
Farnesyl pyrophosphate synthase	Enhanced tolerance to drought stress	[49]
Protein phosphatase 2A	Improved tolerance to drought stress	[49]
RISBZ4	Improved tolerance to drought stress	[49]
Pearl millet		
PgCA	Upregulate PgCA when it exposed to drought condition	[50]
PgGPx	Improved drought and salt in transgenic rice	[58]
PgRab7	Transgenic rice plants displayed to drought and salinity stress	[59]
PgeIF4A	Enhanced tolerance to drought, salinity and oxidative stress in groundnut	[60]

Table 6.
Drought-tolerance genes and their key characteristics in millets.

the same time [61]. Every generation in conventional breeding necessitates time-consuming and costly progeny testing [62]. Resistance genes were introduced into the recurrent parent from the donor parent using marker-assisted breeding. This method can also be used to find the recurrent parent genotype utilising markers that are dispersed over the genome and aren't intimately connected to the target trait [63]. With the use of molecular markers, genes driving the majority of variation in stressed situations like heat and drought have been identified, and field testing has been augmented with marker-assisted selection. The genomic regions that control stress tolerance in plants is known as quantitative trait loci (QTL), and their identification and mapping aids in the early selection or screening of genotypes with stress resistance.

Markers can be used for QTL identification, mapping, and screening as well. Different approaches in molecular breeding for producing water stress-tolerant genotypes include Marker Assisted Selection (MAS), Marker Assisted Backcrossing, Marker Assisted Stacking, and so on (**Figure 4**).

3.4 Transgenic approach

Transgenic techniques require modification of both qualitative and quantitative characters by transferring desired genes [42]. The identification of a specific gene of interest that contributes to water stress tolerance, as well as the transfer of that gene through transgenic breeding, expands the possibilities for crop improvement in drought conditions. Water stress tolerance is induced when a transgene is overexpressed. The engineering of genes that encode growth regulators, suitable solutes, and antioxidants involved in stress tolerance have received the most attention.

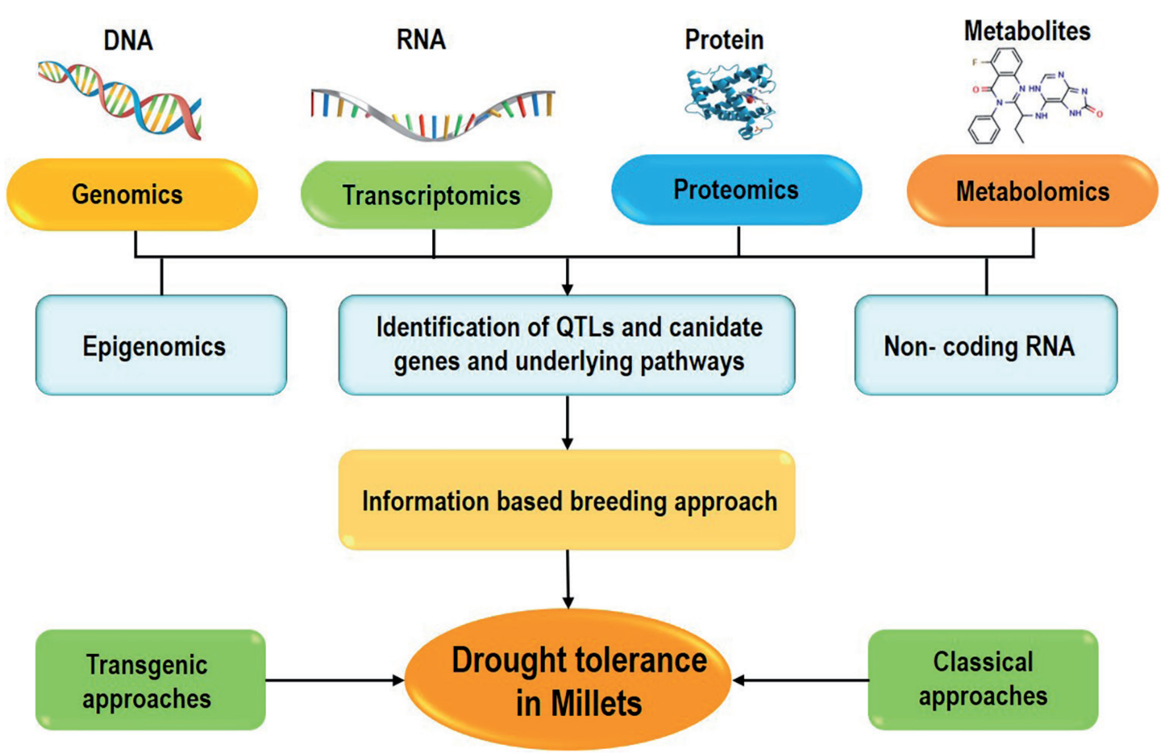

Figure 4.
Schematic representation of the molecular breeding approach for drought tolerance in millets crop.

3.5 Microbe-plant interactions

Microorganisms live in a wide range of environmental conditions, from sub-zero temperatures to desert extremes [64]. Plant-supported phylogenetically varied microbial communities to withstand drought by altering phytohormone levels in the rhizosphere and creating water-sequestering biofilms [65]. Rhizospheric bacteria that lives near plants roots produce a variety of biocontrol chemicals as well as plant growth promoters [66]. These microorganisms are also modifying soil structure, fertility, pH, and oxygen availability [67]. Some other examples of microbes assisted drought tolerance in plants have been listed in **Table 7**.

3.6 Drought resistance in millets: Potential characteristics

Water scarcity and recurrent drought spells in agricultural ecosystems have resulted in considerable yield losses for numerous crops around the world.

Crop	Microbes	Plant part used for isolation	Benefits	References
Foxtail	Actinobacter	Roots	The findings showed that host plants in the rhizoplane enrich specific bacteria and functions.	[68]
Foxtail	*Acinetobacter calcoaceticus* EU- LRNA-72 and *Penicillium sp*	Roots	Increasing glycine betaine, proline, and sugar buildup while lowering lipid peroxidation.	[69]
Foxtail	*Pseudomonas fluorescens*	Roots	Increased soil moisture and improved the root adhering soil/root tissue ratio by efficiently colonising the root adhering soil.	[70]

Table 7.
Drought tolerance in plants were improved by microbes.

Millets Crop	Trait	References
Foxtail	Root structure, grain weight, Dry root weight and root length, root thickness, shoot biomass, root depth, leaf area index, TSS, proline, ABA and JA phytohormones	[29, 30, 31, 35]
Pearl millet	Plant height, biomass, panicle, stalk length, no. of leaves, total grain no. and weight, leaf water potential, rates of stomatal conductance, photosynthesis and transpiration Seed number per ear and ear number per plant number of tiller, harvest index ear, peduncle and ear length and plant height	[23, 27, 31]
Finger millet	Plant height, leaf area total dry matter (TDM), root/shoot ratio by weight and length, grain yield and harvest index	[18, 21, 22, 23]
Barnyard millet	Plant height, leaf area total dry matter (TDM), root/shoot ratio by weight and length, grain yield and harvest index	[24, 25]
Proso millet	Seed number per ear and ear number per plant number of tiller, harvest index ear, peduncle and ear length and plant height	[26, 31]

Table 8.
Potential traits/characters for screening millets crop for drought resistance.

Innovative research results and the rapid development of several unique tools and methodologies in drought-resistance breeding have resulted in significant improvement. However, our understanding of drought resistance in millets crop is still limited, and we know very little about the complex genetic architecture of drought tolerance. We need to uncover the genetic bases of any trait associated with drought resistance in crops that can be used in crop breeding. There are various traits have been used to screen for drought tolerance, including smaller leaf area, leaf area maintenance, water use efficiency, root and shoot biomass, osmotic adjustment, pod number per plant, grain weight, biochemical parameters in millets by different researchers **Table 8** [25, 33, 35, 37, 38, 73].

4. Conclusions

Abiotic stresses are a significant barrier to crop productivity around the world. Plants respond to drought in a variety of ways, the most common of which are changes in plant development and morphology. Crop yields in the past were drastically reduced, according to historical evidence. Drought stress slows crop growth and development, resulting in changes in the crop's morphological, physiological, and biochemical characteristics [10].

Millets play an important role in the livelihood of the developing world's people; on the other hand, have a wide range of coping mechanisms to deal with these challenges. Mostly foxtail millet, pearl millet, proso millet and finger millets perform better tolerance against drought stress [2, 6, 18, 20, 23, 24, 26, 27, 29, 37, 42]. So far, we have studied stress tolerance mechanisms, adaptations, genetic modification, targeted expression of enzymes and transporters, and the role of proline, among other things, in millets [3, 5, 7, 24]. Both traditional and new methods of improvement have yet to be fully adopted. Climate change is expected to have a substantial impact on the types of crops farmed in the coming century.

In future, the key to successful crop improvement will be the ability to identify and access genetic diversity including new or improved variability for target traits by selecting parental germplasm proven to be resilient under likely climate change, including extreme events such as high temperatures [71]. Understanding how millets crops respond to drought stress is therefore essential for drought tolerance breeding. The traditional breeding strategy has demonstrated its ability to sustain productivity growth in numerous crops over the previous century. Meanwhile, current technical breakthroughs have hastened the production of novel cultivars and their impact.

An understanding of the genetic basis of drought tolerance in millets is prerequisite for plant breeders to evolve superior genotypes by adopting biotechnological approaches. There is an urgent need to improve the efficiency of molecular breeding and transgenic approach to develop new and proficient varieties with boosted natural osmolytes and raised tolerance for crops. Additional molecular studies are required to enhance knowledge on proteomic and metabolic activities on millets crop in response to drought stress. The current study's goal was to combine multiple drought tolerance mechanisms and improve these processes in millets crop. Drought stress causes plants to go through morphological, physiological, biochemical, and molecular changes. Changes in leaf structure, root growth, and stomata regulation are all morpho-physiological processes. Changes in phytohormonal levels, such as ABA, JA, Auxins, Ethylene, Gibberellins, Cytokinin, and Brassinosteroids, are biochemical processes. Plant phytohormone levels rise in response to drought, resulting in the activation of morphophysiological and other biochemical processes [72]. Furthermore, emerging ‘omics’ sciences such as genomics, transcriptomics, proteomics, and metabolomics could greatly improve our current understanding of the underlying drought-tolerant candidate genes as well as deciphering the complex gene networks and signalling pathways involved in drought tolerance in millets crop. Importantly, novel strategies like as GE tools and ‘speed breeding’ will aid in a better understanding and effectively speed up the creation of DS-resistant millets crop to reduce the risk of global food instability.

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References

[1] Tadele Z. Drought adaptation in millets. In: Shanker AK, Shanker C, editors. Abiotic and Biotic Stress in Plants—Recent Advances and Future Perspectives [Internet]. London: IntechOpen; 2016

[2] Tiwari A, Rastogi A, Singh V, Arunachalam A. Water stress effects on nutritional values and relative water content of barnyard and finger millet crops. International Journal on Agricultural Sciences. 2019;**10**(1):23-28

[3] Bennetzen JL, Dida MM, Manyera NWM, Devos KM: Characterization of Genetic Diversity in Finger Millet (Eleusine coracana). 2003. Available from: http://www.cerealsgenomics.org/

[4] FAO, FAOSTAT database Rome: Food and Agriculture Organization [Internet]. 2018. Available from: https://www.fao.org/faostat/en/#data/QC. [Accessed: 2020-07-04]

[5] Chandrasekara A, Shahidi F. Effect of food preparation methods on the antioxidant properties of finger millet grain phenolics. Journal of Agricultural and Food Chemistry. 2010;**58**:6706-6714

[6] Tiwari A, Rastogi A, Singh V, Arunachalam A. Effect of water stress on oxidative damage and antioxidant enzyme activity in finger millet and barnyard millet. Indian Journal of Hill Farming. 2020;**33**(1):36-45

[7] Dwivedi S, Upadhyaya H, Senthilvel S, Hash C, Fukunaga K, Diao X, et al. Millets: Genetic and genomic resources. In: Janick J, editor. Plant Breeding Reviews. Hoboken, NJ: John Wiley & Sons; 2012;**35**:247-375. DOI: 10.1002/9781118100509.ch5

[8] Lata C, Gupta S, Prasad M. Foxtail millet: A model crop for genetic and genomic. Critical Reviews in Biotechnology. 2013;**33**(3):328-343

[9] FAO, The World Sorghum and Millet Economies: Facts, Trends and Outlook Part II Millets Introduction [Internet]. 1996. Available from: http://www.fao.org/docrep/W1808E/w1808e0c.htm. [Accessed: 2021-09-18]

[10] Tiwari A, Punetha S, Kesarvani K. Drought stress and its impact on plant mechanism. International Journal of Plant Sciences. 2021;**16**(AAEBSSD):95-112

[11] Kurukulasuriya P, Benhin JKA, Deressa T. Will African agriculture survive climate change? World Bank Economic Review. 2006;**20**(3):367-388

[12] Benhin JKA. South African crop farming and climate change: An economic assessment of impacts. Global Environmental Change. 2008;**18**:666-678

[13] Alexieva V, Sergiev I, Mapelli S, Karanov E. The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. Plant, Cell & Environment. 2001;**24**:1337-1334

[14] Chinnusamy V, Schumaker K, Zhu J. Molecular genetic perspectives on cross- talk and specificity in abiotic stress signalling in plants. Journal of Experimental Botany. 2004;**55**:225-236

[15] Ashraf M, Foolad MR. Roles of glycine betaine and proline in improving plant abiotic stress resistance. Environmental and Experimental Botany. 2006;**59**:206-216

[16] Manivannan P, Jaleel CA, Kishorekumar A, Sankar B,

Somasundaram R, Sridharan R, et al. Changes in antioxidant metabolism of Vigna unguiculata (L.) Walp. By propiconazole under water deficit stress. Colloids and Surfaces. B, Biointerfaces. 2007;**57**(1):69-74

[17] Sankar B, Jaleel CA, Manivannan P, Kishorekumar A, Somasundram R, Panneerselvam R. Drought-induced biochemical modifications and proline metabolism in Abelmoschus esculentus (L.) Moench. Acta Botanica Croatica. 2007;**66**:43-56

[18] Bhatt D, Negi M, Sharma P, Saxena SC, Dobriyal AK. Responses to drought induced oxidative stress in five finger millet varieties differing in their geographical distribution. Physiology and Molecular Biology of Plants. 2011;**17**(4):347-353

[19] Tiwari S, Lata C, Singh Chauhan P, Prasad V, Prasad M. A functional genomic perspective on drought signalling and its crosstalk with phytohormone-mediated signalling pathways in plants. Current Genomics. 2017;**18**(6):469-482

[20] Khatoon H, Singh V. Impact of water stress on physiological and biochemical parameters of finger millet (Eleusine coracana L.). Research in Environment and Life Science. 2016;**9**(12):1474-1477

[21] Tiwari A, Kesarwani K, Ghosh T, Rai S. Declining nutrients from our plates. Research Biotica. 2020;**2**(4):135-140

[22] Aidoo MK, Bdolach E, Fait A, Lazarovitch N, Rachmilevitch S. Tolerance to high soil temperature in foxtail millet (Setaria italica L.) is related to shoot and root growth and metabolism. Plant Physiology and Biochemistry. 2016;**106**:73-81. DOI: 10.1016/j.plaphy.2016.04.038

[23] Maqsood M, Azam Ali SN. Effects of environmental stress on growth, radiation use efficiency and yield of finger millet. Pakistan Journal of Botany. 2006;**39**(2):463-474

[24] Assefa A, Fetene M. Agro-morphological, physiological and yield related performances of finger millet [Eleusine coracana (L.) Gaertn.] accessions evaluated for drought resistance under field condition. Asian Journal of Agriculture and Rural Development. 2013;**3**:709-720

[25] Debieu M, Sine B, Passot S, Grondin A, Akata E, Gangashetty P, et al. Response to early drought stress and identification of QTLs controlling biomass production under drought in pearl millet. PLoS One. 2018;**13**(10):e0201635. DOI: 10.1371/journal.pone.0201635

[26] 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. Pakistan Journal of Botany. 2008;**40**:1427-1432

[27] Subramanian VB, Maheshwari M. Comparison of physiological responses of pearl millet and sorghum to water stress. Proceedings of Indian Academy of Sciences (Plant Sciences). 1989;**99**(6):517-522

[28] Ajithkumar IP, Panneerselvam R. Osmolyte accumulation, photosynthetic pigment and growth of Setaria italica (L.) P. Beauv. Under drought stress. Asian Pacific Journal of Reproduction. 2013;**2**(3):220-224

[29] Liu TY, Ye N, Song T, Cao Y, Gao B, Zhang D, et al. Rhizosheath formation and involvement in foxtail millet (Setaria italica) root growth under drought stress.

Journal of Integrative Plant Biology. 2019;**61**(4):449-462

[30] Ajithkumar IP, Panneerselvam R. ROS scavenging system, osmotic maintenance, pigment and growth status of Panicum sumatrense Roth. Under drought stress. Cell Biochemistry and Biophysics. 2014;**68**(3):587-595

[31] 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. Pakistan Journal of Botany. 2008;**40**:1427-1432

[32] Mahajan S, Tuteja N. Cold, salinity and drought stresses. An overview. Archives of Biochemistry and Biophysics. 2006;**444**:139-158

[33] Shivhare R, Asif MH, Lata C. Comparative transcriptome analysis reveals the genes and pathways involved in terminal drought tolerance in pearl millet. Plant Molecular Biology. 2020;**103**(6):639-652. DOI: 10.1007/s11103-020-01015-w

[34] Mundada PS, Nikam TD, Kumar SA, Umdale SD, Ahire ML. Morpho-physiological and biochemical responses of finger millet (Eleusine coracana (L.) Gaertn.) genotypes to PEG-induced osmotic stress. Biocatalysis and Agricultural Biotechnology. 2020;**23**:101488

[35] Xu BQ, Gao XL, Gao JF, Li J, Yang P, Feng BL. Transcriptome profiling using RNA-seq to provide insights into foxtail millet seedling tolerance to short-term water deficit stress induced by PEG-6000. Journal of Integrative Agriculture. 2019;**18**(11):2457-2471

[36] Vijayalakshmi T, Varalaxmi Y, Jainender S, Yadav SK, Vanaja M. Physiological and biochemical basis of water-deficit stress tolerance in pearl millet hybrid and parents. American Journal of Plant Science. 2012;**3**:1730-1740

[37] Henson IE, Mahalakshmi V, Alagarswamy G, Bidinger FR. Leal abscisic acid content and recovery from water stress in pearl millet (Pennisetum americanum (L.) Leeke). Journal of Experimental Botany. 1984;**35**:99-109

[38] Shivhare R, Lata C. Assessment of pearl millet genotypes for drought stress tolerance at early and late seedling stages. Acta Physiologiae Plantarum. 2019;**41**(3):39

[39] Qi X, Xie S, Liu Y, Yi F, Yu J. Genome-wide annotation of genes and noncoding RNAs of foxtail millet in response to simulated drought stress by deep sequencing. Plant Molecular Biology. 2013;**83**:459-473

[40] Wang M, Li P, Li C, Pan Y, Jiang X, Zhu D, et al. SiLEA14, a novel atypical LEA protein, confers abiotic stress resistance in foxtail millet. BMC Plant Biology. 2014;**14**(1):290

[41] Li C, Yue J, Wu X, Xu C, Yu J. An ABA-responsive DRE-binding protein gene from Setaria italica, SiARDP, the target gene of SiAREB, plays a critical role under drought stress. Journal of Experimental Botany. 2014;**65**(18):5415-5427

[42] Yu TF, Zhao WY, Fu JD, Liu YW, Chen M, Zhou YB, et al. Genome-wide analysis of CDPK family in foxtail millet and determination of SiCDPK24 functions in drought stress. Frontiers in Plant Science. 2018;**9**:541

[43] Pan Y, Li J, Jiao L, Li C, Zhu D, Yu J, et al. A non-specific Setaria italica L. lipid transfer protein gene plays a critical

role under abiotic stress. Frontiers. Plant Science. 2016;**7**:1752

[44] Li WW, Chen M, Zhong L, Liu JM, Xu ZS, Li LC, et al. Overexpression of the autophagy-related gene SiATG8a from foxtail millet (Setaria italica L.) confers tolerance to both nitrogen starvation and drought stress in Arabidopsis. Biochemical and Biophysical Research Communications. 2015;**468**(4):800-806

[45] Feng ZJ, He GH, Zheng WJ, Lu PP, Chen M, Gong YM, et al. Foxtail millet NF-Y families: Genome-wide survey and evolution analyses identified two functional genes important in abiotic stresses. Frontiers in Plant Science. 2015;**6**:1142

[46] Feng ZJ, Xu ZS, Sun J, Li LC, Ming C, Yang GX, et al. Investigation of the ASR family in foxtail millet and the role of ASR1 in drought/oxidative stress tolerance. Plant Cell Reports. 2016;**35**:115-128

[47] Li J, Dong Y, Li C, Pan Y, Yu J. SiASR4, the target gene of SiARDP from Setaria italica, improves abiotic stress adaption in plants. Frontiers in Plant Science. 2017;**7**:2053

[48] Xu W, Tang W, Wang C, Ge L, Sun J, Qi X, et al. SiMYB56 confers drought stress tolerance in transgenic rice by regulating lignin biosynthesis and ABA signaling pathway. Frontiers in Plant Science. 2020;**11**:785

[49] Singh RK, Singh VK, Raghavendrarao S, Phanindra MLV, Raman KV, Solanke AU, et al. Expression of finger millet EcDehydrin7 in transgenic tobacco confers tolerance to drought stress. Applied Biochemistry and Biotechnology. 2015;**177**(1):207-216

[50] Bhatt D, Saxena SC, Jain S. Cloning, expression and functional validation of drought inducible ascorbate peroxidase (Ec-apx1) from Eleusine coracana. Molecular Biology Reports. 2013;**40**(2):1155-1165

[51] Babitha KC, Vemanna RS, Nataraja KN, Udayakumar M. Overexpression of EcbHLH57 transcription factor from Eleusine coracana L. in tobacco confers tolerance to salt, oxidative and drought stress. PLoS One. 2015;**10**:e0137098

[52] Babitha KC, Ramu SV, Nataraja KN, Sheshshayee MS, Udayakumar M. EcbZIP60, a basic leucine zipper transcription factor from Eleusine coracana L. improves abiotic stress tolerance in tobacco by activating unfolded protein response pathway. Molecular Breeding. 2015;**35**:181

[53] Ramegowda V, Gill US, Sivalingam PN, Gupta A, Gupta C, Govind G, et al. GBF3 transcription factor imparts drought tolerance in Arabidopsis thaliana. Scientific Reports. 2017;**7**:9148

[54] Chopperla R, Singh S, Sangala R, Padaria JC, Mohanty S, Sharma TR, et al. The membrane tethered transcription factor EcbZIP17 from finger millet promotes plant growth and enhances tolerance to abiotic stresses. Scientific Reports. 2018;**8**:2148

[55] Hema R, Vemanna RS, Sreeramulu S, Reddy CP, Senthil KM, Udayakumar M. Stable expression of mtlD gene imparts multiple stress tolerance in finger millet. PLoS One;**9**:e99110

[56] Sreekumar PM, Nataraja KN, Yashoda BK, Ramegowda HV, Mamrutha HM, Rama N. Expression analysis of stress responsive pathway genes linked to drought hardiness in an adapted crop, finger millet (Eleusine coracana). Journal of Plant Biochemistry and Biotechnology. 2013;**22**(2):193-201

[57] Kaul T, Reddy PS, Mahanty S, Thirulogachandar V, Reddy RA, Kumar B, et al. Biochemical and molecular characterization of stress-induced beta-carbonic anhydrase from a C (4) plant, Pennisetum glaucum. Journal of Plant Physiology. 2011;**168**(6):601-610

[58] Islam T, Manna M, Reddy MK. Glutathione peroxidase of Pennisetum glaucum (PgGPx) is a functional Cd2+ dependent peroxiredoxin that enhances tolerance against salinity and drought stress. PLoS One. 2015;**10**:e0143344

[59] Tripathy MK, Tiwari BS, Reddy MK, Deswal R, Sopory SK. Ectopic expression of PgRab7 in rice plants (Oryza sativa L.) results in differential tolerance at the vegetative and seed setting stage during salinity and drought stress. Protoplasma. 2017;**254**:109-124

[60] Rao TSRB, Naresh JV, Reddy S, Reddy MK, Mallikarjuna G. Expression of Pennisetum glaucum eukaryotic translational initiation factor 4A (PgeIF4A) confers improved drought, salinity, and oxidative stress tolerance in groundnut. Frontiers in Plant Science. 2017;**8**:453

[61] Varshney RK, Singh VK, Kumar A, Powell W, Sorrells ME. Can genomics deliver climate-change ready crops. Current Opinion in Plant Biology. 2018;**45**:1-7

[62] Lema M. Marker assisted selection in comparison to conventional plant breeding: Review article. Agricultural Research and Technology. 2018;**14**(2):1-10

[63] Collard BCY, Jahufer MZZ, Brouwer JB, Pang ECK. An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: The basic concepts. Euphytica. 2005;**142**(2):169-196

[64] Xue J, Yu Y, Bai Y, Wang L, Wu Y. Marine oil-degrading microorganisms and biodegradation process of petroleum hydrocarbon in marine environments: A review. Current Microbiology. 2015;**71**:220-228

[65] Bhattacharyya A, Pablo CHD, Mavrodi OV, Weller DM, Thomashow LS, Mavrodi DV. Rhizosphere plant-microbe interactions under water stress. Advances in Applied Microbiology. 2021;**115**:65-113. DOI: 10.1016/bs.aambs.2021.03.001

[66] Ullah A, Manghwar H, Shaban M, Khan AH, Akbar A, Ali U, et al. Phytohormones enhanced drought tolerance in plants: A coping strategy. Environmental Science and Pollution Research. 2018;**25**:33103-33118

[67] Finkel OM, Castrillo G, Paredes SH, González IS, Dangl JL. Understanding and exploiting plant beneficial microbes. Current Opinion in Plant Biology. 2017;**38**:155-163

[68] Jin T, Wang Y, Huang Y, Xu J, Zhang P, Wang N. Taxonomic structure and functional association of foxtail millet root microbiome. Gigascience. 2017;**6**:1-12. DOI: 10.1093/gigascience/gix089

[69] Kour D, Rana KL, Yadav AN, Sheikh I, Kumar V, Dhaliwal HS, et al. Amelioration of drought stress in foxtail millet (Setaria italica L.) by P-solubilizing drought-tolerant microbes with multifarious plant growth promoting attributes. Environmental Sustainability. 2020;**3**:23-34

[70] Niu X, Song L, Xiao Y, Ge W. Drought-tolerant plant growth promoting rhizobacteria associated with foxtail millet in a semiarid agroecosystem

and their potential in alleviating drought stress. Frontiers in Microbiology. 2018;**8**:2580

[71] Newton AC, Johnson SN, Gregory PJ. Implications of climate change for diseases, crop yields and food security. Euphytica. 2011;**179**:3-18

[72] Ilyas M, Nisar M, Khan N, Hazrat A, Khan AM, Hayat K, et al. Drought tolerance strategies in plants: A mechanistic approach. Journal of Plant Growth Regulation. 2021;**40**(3):926-944

[73] Yu A, Zhao J, Wang Z, Tian G, Liu X, Guo E, et al. Transcriptome and metabolite analysis reveal the drought tolerance of foxtail millet significantly correlated with phenylpropanoids-related pathways during germination process under PEG stress. BMC Plant Biology. 2021;**20**:274. DOI: 10.1186/s12870-020-02483-4