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Drought Adaptation in Millets

Zerihun Tadele

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Abstract

Millets are major food and feed sources in the developing world especially in the semi-arid tropical regions of Africa and Asia. The most widely cultivated millets are pearl millet [*Pennisetum glaucum* (L.) R. Br.], finger millet [*Eleusine coracana* (L.) Gaertn], foxtail millet [*Setaria italica* (L.) P. Beauvois], Japanese barnyard millet [*Echinochloa esculneta* (A. Braun) H. Scholz], Indian Barnyard millet [*Echinochloa frumetacea* Link], kodo millet [*Paspalum scrobiculatum* L.], little millet [*Panicum sumatrense* Roth.ex.Roem. & Schult.], proso millet [*Panicum miliaceum* L.], tef [*Eragrostis tef* (Zucc.) Trotter] and fonio or acha [*Digitaria exilis* (Kippist) Stapf and *D. iburua* Stapf]. Millets are resilient to extreme environmental conditions especially to inadequate moisture and are rich in nutrients. Millets are also considered to be a healthy food, mainly due to the lack of gluten (a substance that causes coeliac disease) in their grain. Despite these agronomic, nutritional and health-related benefits, millets produce very low yield compared to major cereals such as wheat and rice. This extremely low productivity is related to the challenging environment in which they are extensively cultivated and to the little research investment in these crops. Recently, several national and international initiatives have begun to support the improvement of diverse millet types.

Keywords: Abiotic stress, drought avoidance, drought escape, drought tolerance, millet

1. Introduction

Millets are among the major cereal crops in the developing world especially in the semi-arid tropical regions of Africa and Asia where they are used both as human food and livestock feed. Millets represent small grain crops that are mainly cultivated in marginal environments. Exceptional to this definition is pearl millet [*Pennisetum glaucum* (L.) R. Br.] that has a large seed size. Among the widely cultivated millets, those traditionally considered as millet are pearl millet, finger millet [*Eleusine coracana* (L.) Gaertn], foxtail millet [*Setaria italica* (L.) P. Beauvois], Japanese barnyard millet [*Echinochloa esculneta* (A. Braun) H. Scholz], Indian

Barnyard millet [*Echinochloa frumetacea* Link], kodo millet [*Paspalum scrobiculatum* L.], little millet [*Panicum sumatrense* Roth ex Roem. & Schult.] and proso millet [*Panicum miliaceum* L.] (Table 1). Tef [*Eragrostis tef* (Zucc.) Trotter] was included in the millet group at the First Small Millets Workshop held 30 years ago in Bangalore, India [1], while both tef and fonio or acha [*Digitaria exilis* (Kippist) Stapf and *D. iburua* Stapf] were grouped under small millets by international agricultural organizations in the mid-1990s [2]. The inclusion of tef and fonio to the millet family is justifiable due to the close relationship of the two species with other millets. The genetic difference between some traditional millets is as large as that between tef or fonio and other millets. Due to this substantial variability among themselves, millets are grouped into two subfamilies, namely Panicoideae, which includes pearl millet, foxtail millets, Japanese barnyard millet and Indian millet, and to Chloridoideae, which includes finger millet and tef, and eight genera (Table 1). This indicates that finger millet which is normally grouped under millet is more closely related to tef than to other millets [3]. The divergence among traditional millets is also exhibited in the chromosome number and ploidy level which range from the diploid pearl millet ($2n = 2x = 14$) to the hexaploid fonio ($2n = 6x = 54$) [4, 5]. Millets are also divergent in the size and colour of seeds, seed weight, plant stature and shape of their panicles (Table 1). The geographical distributions of small millets were recently summarized by Goron and Raizada [6]. Except for finger millet, which is extensively cultivated in Africa and Asia, other small millets are mainly grown in Asia.

Common name	Traditional millets				
	Pearl millet	Foxtail millet	Japanese Barnyard millet	Indian Barnyard millet	Kodo millet
Other names	Bulrush millet	Italian millet	Japanese millet	Billion dollar grass	Koda millet
Botanical names	<i>Pennisetum glaucum</i>	<i>Setaria italica</i>	<i>Echinochloa esculneta</i>	<i>Echinochloa frumetacea</i>	<i>Paspalum scrobiculatum</i>
Subfamily	Panicoideae	Panicoideae	Panicoideae	Panicoideae	Panicoideae
Tribe	Paniceae	Paniceae	Paniceae	Paniceae	Paniceae
Distribution			Japan, Korea, China	India, Pakistan, Nepal	
Ploidy level	Diploid	Diploid	Hexaploid	Hexaploid	Tetraploid
Chromosome number	$2n = 2x = 14$	$2n = 2x = 18$	$2n = 6x = 36$	$2n = 6x = 36$	$2n = 4x = 40$
Purpose	Food, feed	Food, biofuel	Food, feed	Food	Food, feed
Agronomic benefits	Drought & heat tolerance	Drought tolerance	Early maturity, anti-fungal	Early maturity	Drought tolerance
Nutritional benefits	High protein, starch & minerals		anti-diabetic	High protein content	High-quality protein
Health benefits	No gluten	No gluten	No gluten	No gluten	Low glycaemic index, anti-oxidant
Reference	[4, 20, 27]	[16, 27]	[5, 18, 27]	[6]	[27, 36]

Common name	Traditional millets			Other millets	
	Little millet	Proso millet	Finger millet	Tef	Fonio
Other names		Common millet	Ragi, African millet	Teff, lovegrass	Acha
Botanical names	<i>Panicum sumatrense</i>	<i>Panicum miliaceum</i>	<i>Eleusine coracana</i>	<i>Eragrostis tef</i>	<i>Digitaria exilis</i> , <i>D. Iburua</i>
Subfamily	Panicoideae	Panicoideae	Chloridoideae	Chloridoideae	Panicoideae
Tribe	Paniceae	Paniceae	Eragrostideae	Eragrostideae	Paniceae
Distribution					
Ploidy level	Tetraploid	Tetraploid	Tetraploid	Tetraploid	Diploid or hexaploid
Chromosome number	$2n = 4x = 36$	$2n = 4x = 36$	$2n = 4x = 36$	$2n = 4x = 40$	$2n = 2x = 30$ or $2n = 6x = 54$
Purpose	Food	Food, feed	Food, feed	Food, feed	Food, feed
Agronomic benefits	Abiotic stress tolerance	Drought tolerance, early maturity	Drought and salt tolerance	Water-logging tolerance, storage pest tolerance	Drought tolerance
Nutritional or	High in phytochemicals, fibre	Rich in amino acids	Rich in calcium, methionine and tryptophan	Rich in protein	Rich in amino acids
Health benefits	Anti-diabetic	Anti-cancer	Low glycaemic index, anti-oxidant	No gluten	
Reference	[38–40]	[6, 23, 27]	[6, 20, 27, 35, 37]	[33, 47]	[20, 24, 25]

Table 1. Description and benefits of millets

2. Importance of millets in global agriculture

2.1. Economic benefits

Millets play a key role in the economy of the developing world especially in countries with extensive areas of marginal land used for crop cultivation. In 2013, the global area under millet cultivation was 34.9 million hectares, corresponding to 4.7 % of the global area for all cereals including wheat, maize and rice [7] (Table 2). On the other hand, the global production of millets in the same year was estimated to be 36.7 million tons, which contributes only 1.2% to the total cereal production. This lower production was due to the inferior average yield of millets (only 0.9 t ha⁻¹) compared to other cereals (3.8 t ha⁻¹). However, the contribution of India to global millet production is significant. In 2013, India produced over 30% of the global millet yield from only 25% of the global millet area, mainly due to improved productivity. In the same year, while the mean seed yield of millet in India was 1.2 t ha⁻¹, it was only 0.8 t ha⁻¹ for other countries. This 50% production advantage in India over other countries especially African countries was due to the widespread use of improved varieties and techniques. A

decade ago, the rate of adoption of improved pearl millet cultivars by farmers was 65% in India but below 10% in some African countries [8].

Country	Traditional millets ^a	Tef	Fonio (Acha)	Total
Production (ton)				
India	10,910,000			10,910,000
Ethiopia	848,956 ^b	4,418,642		5,267,598
Nigeria	5,000,000		90,000	5,090,000
Niger	2,995,000		6,000	3,001,000
China	1,746,000			1,746,000
Mali	1,152,331		22,090	1,174,421
Burkina Faso	1,078,570		19,887	1,098,457
Sudan (former)	1,090,000			1,090,000
Guinea	215,000		429,000	644,000
Chad	582,000			582,000
Senegal	572,155		1,030	573,185
Russia	418,844			418,844
USA	418,145			418,145
Tanzania	322,731			322,731
Pakistan	310,000			310,000
Nepal	305,588			305,588
Uganda	228,000			228,000
Myanmar	185,000			185,000
Ghana	155,131			155,131
Cameroon	97,000			97,000
others	1,233,696		19,000	1,252,696
Total production	29,864,147	4,418,642 ^c	587,007	34,869,796
Total area (ha)	33,118,792	3,016,521	554,451	36,689,764
Yield (ton ha⁻¹)^d	0.90	1.47	1.06	0.95
Reference	[7,9]	[9]	[7]	

^a Traditional millets include finger millet, foxtail millet, Indian barnyard millet, Japanese barnyard millet, kodo millet, little millet, pearl millet and proso millet.

^b Only for finger millet.

^cOnly for Ethiopia.

^d Average global yield except for tef where it is the national average yield for Ethiopia.

Table 2. The top 20 millet-producing countries in the world in 2013.

Tef and fonio are exclusively cultivated in Africa. While fonio is cultivated on a total of half a million hectares in West Africa mainly in Guinea, Guinea-Bissau and Côte d'Ivoire [7], tef is grown in the Horn of Africa especially in Ethiopia where it is annually cultivated on three million hectares of land and is a staple food for about 50 million people [9]. In the last two decades, the productivity of tef was raised by 100%, from just 0.7 t ha⁻¹ in 1994 to 1.4 t ha⁻¹ in 2013 mainly due to an increase in the use of improved cultivars.

In general, millets play a key role in food security in Asia and Africa. Together with sorghum, millets account for about half of the total cereal production in Africa [10]. Millets, are therefore considered as a poor man's crop due to their significant contributions to the diet of resource-limited farmers and consumers.

2.2. Agronomic benefits

Millets are resilient to the extreme climatic and soil conditions prevalent in the semi-arid regions of Asia and Africa. The similarities of millets are that they are all grown under extreme environmental conditions, especially those of inadequate moisture and poor soil fertility which are poorly suited to the major crops of the world [11] (Table 1). Proso millet is considered to have been domesticated before rice in China, based on the extreme resistance of this millet to drought [12, 13]. In addition to its resistance to drought, proso millet escapes the terminal drought that normally occurs late in the growing season since it matures in only three months; hence, proso millet is considered to be a millet with low water requirements [6].

Similar to maize and sorghum, millets possess a C₄ photosynthesis system [14, 15]; hence, they prevent photorespiration and, as a consequence, efficiently utilize the scarce moisture present in the semi-arid regions. Since C₄ plants are able to close their stomata for long periods, they can significantly reduce moisture loss through the leaves. In addition to its tolerance to drought, tef is tolerant to waterlogging especially in poorly drained soils where other crops such as maize and wheat could not survive. Foxtail millet is also considered to be a model plant for biofuel studies [16]. A novel peptide isolated from foxtail millet and barnyard millet has shown strong antifungal properties as has one from finger millet which is especially effective and works against four fungus species, namely *Alternaria*, *Trichoderma*, *Botrytis* and *Fusarium* [17, 18].

2.3. Nutritional benefits

Millets are rich sources of nutrients for both humans and animals. Saleh et al. [19] have compiled detailed information on the nutritional advantages of several millets. The grains of most millets possess levels of protein comparable to those of wheat but higher than those of rice [20] (Table 1). In addition, the seeds of finger millet contain valuable amino acids especially methionine [20], which is lacking in the diets of hundreds of millions of the poor who live on starchy staples such as cassava. Other reports indicate that finger millet is rich in lysine, threonine and valine [21, 22] while proso millet has plentiful leucine, isoleucine and methionine [23]. The seeds of fonio are also nutritious, especially in amino acids such as leucine, methionine and valine [24, 25]. Since proso millet is rich in essential amino acids

including leucine, isoleucine and methionine, the protein quality of the grain is higher than that of wheat [23].

The grains of extensively cultivated pearl millet contain high amounts of starch, fibres and minerals [26, 27]. In general, millets have high amounts of vitamins, calcium, iron, potassium, magnesium and zinc [28].

The straws and crop residues of millets are also the main source of livestock feed for farmers in developing countries. In Ethiopia, compared to the straw from other cereals, the straw of tef is the most palatable to livestock and fetches the highest price [29].

2.4. Health-related benefits

In addition to being nutritious, millets are also considered to be a healthy food. Two recent reviews examined the health-related benefits associated with millets [19, 6]. A number of leading newspapers and media have recently indicated the potential of millets particularly tef as a global lifestyle crop [30–32]. This is particularly due to the lack of gluten in the grain of tef [33] (Table 1). Gluten is a substance present in wheat and other grains that causes celiac disease or other forms of allergies. Similar to tef, several other millets, particularly foxtail millet, do not contain gluten.

Six millet species (namely kodo, finger, proso, foxtail, little and pearl millets) were shown to have an anti-proliferative property and might have a potential in the prevention of cancer initiation [34, 35]. The anti-proliferative property of these millets is associated with the presence of phenolic extracts. Among the first four millets indicated above, the maximum phenolic content was obtained in kodo millet while the minimum was in foxtail millet [36].

Finger millet is also a popular food among diabetic patients because of its low glycaemic index and slow digestion due to high fibre content [37]. The glycaemic index of little millet was also lower than that of rice, wheat and sorghum; hence, it is considered to be an anti-diabetic grain [38]. The composition of useful antioxidants and related products could be enhanced through processing the grain. A study in little millet showed that the levels of phenolics, flavonoids and tannins were substantially increased by germinating, steaming and roasting soaked grains [39].

3. Drought: A major challenge to millet cultivation

Biotic stresses such as insect pests and diseases are a cause for substantial yield losses to diverse types of millets. However, abiotic stresses are the biggest contributor to losses every year. Although, in general, millets perform better than cereals such as wheat and rice in semi-arid environments, these challenging climatic and soil conditions are by no means an optimum environment for millet cultivation. In semi-arid and arid environments where millets are the dominant crop, drought or inadequate moisture is the major abiotic stress affecting productivity. Studies in pearl millet showed that drought impacts include growth, yield, membrane integrity, pigment, osmotic adjustment, water relations and photosynthetic activity [40].

3.1. Prevalence of drought

Drought is defined as a temporary reduction in moisture availability in which the amount of available water is significantly below normal for a specified period. In general, drought can be explained as meteorological, hydrological or agricultural drought [41]. Agricultural drought occurs when there is not enough soil moisture to meet the needs of a particular crop at a particular time. Drought is also commonly expressed as a shortage or absence of rainfall causing a loss in rain-fed agriculture. For example, the decline in the level of rainfall during severe drought years in Ethiopia was accompanied by serious reductions in rain-fed agricultural outputs; this is because a 10% drop in rainfall (below the long-term national averages) results in an average drop of 4.2% in cereal yields [42].

As indicated above, millets are crops of dry land areas of the world. According to the United Nations, dry lands, which cover 40% of the world's land area or one-third of the global arable land, support two billion people, of which 90% live in the developing world [43]. Dry lands are classified into four, namely hyper-arid deserts, arid, semi-arid and dry subhumid. Millets are extensively cultivated in the semi-arid region, which is characterized by low and erratic rainfall and periodic drought. Climate change is expected to worsen the situation in this part of the world by reducing the grassland productivity by 49–90% by 2020 [43]. The Sahel Region in Africa, covering over three million km² in 10 countries (namely northern Senegal, southern Mauritania, central Mali, northern Burkina Faso, the extreme south of Algeria, Niger, the extreme north of Nigeria, central Chad, central and southern Sudan and northern Eritrea) is the typical semi-arid region situated between the Sahara desert in the north and the tropical or savanna climate in the south [44].

The frequency and intensity of drought has increased in recent times. In Ethiopia, severe droughts used to occur periodically every 6–8 years [45], but recently, they have happened every 1–2 years especially in the south of the country [46].

Similar to other millets, drought is implicated among the major yield limiting factors in tef production [47]. Although tef grows in a wide variety of agro-ecological conditions ranging from semi-arid areas with low rainfall to areas with high rainfall, the rainfall pattern in most tef growing regions is not consistent enough to support the normal growth of the crop during the crop cycle. In most tef growing regions, greater rainfall variability exists over the growing period than over the year-cycle [48, 49] which results in poor agricultural outputs. The Water Requirement Satisfaction Index (WRSI), a crop-specific performance indicator taking rainfall and soil characteristics into account, indicates extreme and increasing variability in Ethiopia. A recent study also confirmed that climate will have a negative impact on the acreage and productivity of tef unless urgent interventions are implemented which favours mitigation and adaptation strategies [50].

3.2. Yield losses due to drought

Various yield loss studies made for millets treated with drought conditions are summarized in Table 3. Using polyvinylchloride (PVC) tubes filled with sandy soil, Matsuura and colleagues [51] investigated the effect of moisture deficit before and after flowering on four millets,

namely proso millet, little millet, foxtail millet and wild millet [*Setaria glauca* (L.) Beauv.]. Compared to the well-watered plants, a significant yield reduction was obtained in all four millets when the drought treatment was implemented at early developmental stage, that is, before flowering (or heading). However, terminal drought, which occurs from the flowering stage to the harvesting of the crop, contributed to a significant yield loss only in proso and little millets while the effect on foxtail and wild millets was negligible.

Millet type	Yield loss (%)			Critical stage	Reference
	Early drought ^a	terminal drought ^b	Long-term drought ^c		
Proso millet	30.1*	34.6*	64.0*	Before and after heading	[51]
Little millet	62.6*	80.1*	80.5*		[51]
Foxtail millet	19.2*	3.4 ^{NS}	20.3*	Before heading	[51]
Wild millet (<i>Setaria glauca</i>)	27.3*	15.3 ^{NS}	30.1*		[51]
	Mid-season stress ^d	Terminal stress ^e			
Pearl millet	6.6	60.1		Flowering	[53]
Finger millet		109.8 ^{ff}		Flowering	[54]
	Prior to flowering	Beginning flowering	End of flowering		
Pearl millet	72	61	Insignificant	From four weeks to flowering	[52]
	Early stress ^g				
Tef	69–77				[55]

^a Early drought: water stress from 25 days after sowing till flowering.

*Indicates statistically significant difference from the well-watered samples.

^b Terminal drought: water stress from flowering till harvesting.

^c Long-term drought: water stress from 25 days after sowing till harvesting.

^d Mid-season stress: water stress for 30 days from floral initiation to flowering.

^eTerminal stress: water stress at flowering.

^f Water stress from 28 days after sowing to harvest.

^g Early stress: water stress from two weeks after emergence until symptoms of stress observed.

Table 3. The magnitude of yield loss due to moisture scarcity in millets.

A study by Winkel et al. [52] in Niger where the annual rainfall is around 200 mm investigated the impact of water deficit at three stages of pearl millet development. The three stages were prior to flowering, at flowering and at the end of flowering. According to the findings of the work, the grain yield of pearl millet was severely reduced when moisture was limited prior to

and at the flowering stage but not at the end of flowering. On the other hand, in pearl millet, terminal drought in which irrigation was terminated from the flowering until crop maturity, was severe, as it resulted in 60% yield loss [53]. The mid-season stress, which occurred from one month before flower initiation to full flowering, resulted in only 7% yield loss.

The study in two landraces of finger millet in which a drought treatment was imposed four weeks after sowing, resulted in 100% yield loss and over 30% biomass damage [54]. Similarly, yield loss reached up to 77% when the tef plant experienced drought at the flowering stage [55].

Although yield loss studies were not exhaustively made for most millets as they are considered drought tolerant, substantial damage occurs to these crops depending on the severity of drought. However, millets produce at least some grain and straw even in bad years unlike drought-intolerant cereals such as wheat and rice which completely fail to produce any yield.

4. Adaptation of millets to drought

4.1. Strategies to drought adaptation or tolerance

Plants cope with drought using three main strategies, namely, drought escape, drought avoidance and drought tolerance, although a fourth strategy, known as drought recovery, has also been identified [56–60].

Drought escape: Drought escape refers to the condition in which plants reach maturity before the drought occurs. Traits associated with drought escape are rapid growth, early flowering, high leaf nitrogen level and high photosynthetic capacity [58]. The study in West Africa indicated that pearl millet matches its phenology to the mean distribution of the rainfall where precipitation is limited and erratic [61]. In this case, the development of the main panicle coincided with an increasing period of rain, thus reducing the risks associated with drought events occurring prior to or at the beginning of flowering.

Drought avoidance: Drought avoidance refers to the ability of the plant to maintain a favourable water balance under moisture stress in order to avoid water deficit in the plant tissue. Two types of drought avoidance mechanisms have been identified: (i) those that reduce water loss through transpiration (e.g. low stomata conductance and reduced leaf) and (ii) those that maintain water uptake during drought period (e.g. high root-to-shoot ratio) [56, 58, 62].

Drought tolerance: Drought tolerance refers to the ability of the plant to produce some yield by withstanding low water potential [62]. Traits associated with drought tolerance are increased osmoprotectants (or compatible solutes such as betaines and amino acids), and osmotic adjustment (i.e. reducing osmotic potential through accumulation of organic and inorganic substances) [58, 60].

Drought recovery: Drought recovery refers to a condition in which plants recover from the adverse effects of drought in order to provide some yield and/or biomass. Desiccation-tolerant or resurrection plants particularly the wild *Eragrostis nindensis* is the typical example of drought recovery since it stabilizes its cells or membranes at desiccated state [63].

These strategies which are devised by plants to cope with drought are manifested through changes in some phenotypic traits. In a recent review, Kooyers [58] showed for each strategy the path followed by plants in terms of life cycle, altered phenotypes and to the type of drought the plant fits itself. This indicates that the strategies and mechanisms of drought tolerance are interrelated.

4.2. Mechanism of drought tolerance

Table 4 summarizes various mechanisms of drought tolerance in diverse millet types. These inherent properties of plants which include agronomical, morphological and physiological traits are briefly discussed below.

Parameter	Millet type	Response to drought	Reference
Agronomy-related traits			
Seed number and biomass	Pearl millet	Unaffected under drought	[64]
Seed yield	Pearl millet	High for drought-tolerant genotypes	[65]
Flowering time	Pearl millet	Adjust phenology to rainfall pattern	[53]
Morphology-related traits			
Shoot length	Little millet	Decreased under drought	[40]
Root length	Little millet	Increased under drought	[40]
Leaf tensile strength	Tef	Increased in drought-tolerant plants	[68]
Physiology-related traits			
Water extraction	Pearl millet	Less extraction before flowering; more extraction after flowering	[65]
Chlorophyll content	Little millet	Decreased under drought	[40]
Biochemical-related traits			
Anti-oxidants	Little millet	Accumulated under drought	[40]
ROS scavenging enzymes	Little millet, tef	Accumulated under drought	[40, 71]
Free proline	Tef, little millet	Increased concentration	[40, 71]
GB (glycine betaine)	Little millet	Accumulated under drought	[40]
Superoxide	Little millet	Accumulated under drought	[40]
AP (ascorbate peroxidase)	Tef, little millet	Increased specific activity	[40, 71]
CAT (catalase)	Little millet	Accumulated under drought	[40]
GR (glutathione reductase)	Tef	Increased concentration	[71]
MDAR (monodehydro-ascorbate reductase)	Tef	Increased concentration	[71]
Total free amino acid	Little millet	Increased concentration	[40]

Table 4. Traits associated to diverse drought tolerance mechanisms in millets.

Agromony-related traits: These refer to the traits that are commonly known as yield and yield components. Among these, number of tillers, number and size of panicle, seed and biomass yield, seed weight and harvest index are the major ones. However, conclusions could not be made from the two studies using drought-tolerant pearl millet cultivars since drought did not affect the shoot biomass in the first case [64] while it boosted the seed yield in the second case [65].

Morphology-related traits: Morphological or anatomical traits which play important roles in drought tolerance include root- and shoot length and leaf area [66]. However, changes in the morphological and biochemical properties of the flag leaf play a key role in drought tolerance as flag leaves are the primary source of photosynthesis [67]. Mechanical properties of the plant also affect drought tolerance in millets. Balsamo et al. [68] studied the leaf tensile strength or also known as force to tear in three *Eragrostis* species with different levels of tolerance to drought. According to their findings, drought-tolerant *E. curvula* had higher tensile strength values than the moderately drought-tolerant *E. tef*, which in turn had higher values than the drought-susceptible *E. capensis*, indicating a positive correlation between drought tolerance and leaf tensile strength [68]. Structural investigations of leaves from the three species revealed the presence of extensive lignification of bundle sheath extensions in *E. tef* and *E. curvula* unlike in *E. capensis*. A study in maize indicated that lignification of the midrib parenchyma and epidermis was directly correlated with increased tensile strength [69].

Physiology-related traits: Among the several physiological traits that are differentially regulated during moisture deficit, osmotic adjustment is a major mechanism that increases drought avoidance to enable the plant produce some yield. Osmotic adjustment, which refers to the lowering of the osmotic potential in the cytoplasm due to the accumulation of compatible solutes such as proline, glycine betaine and organic acids, contributes to turgor maintenance of shoots and roots [40]. In little millet, drought stress increased the amount of proline and glycine betaine in both the root and leaf [40]. According to the authors, the accumulation of free amino acids in this millet during drought might be related to the disruption in protein synthesis, induced proteolysis or its partial hydrolysis [40]. Water-use efficiency of the plant is also important as moisture is mostly limited in the areas where millets are extensively cultivated. The experiment using drought-sensitive and drought-tolerant pearl millet genotypes showed that under moisture deficit conditions, the total amount of water extracted by both genotypes was comparable [65]. However, compared to susceptible genotypes, tolerant genotypes extracted less water prior to flowering and more water after flowering, enabling these genotypes to support the tillers and maintain the stay-green phenotype.

Biochemical-related traits: Reactive oxygen species (ROS) are chemically reactive molecules that are useful in cell signalling at low concentrations but are damaging to cells when present at high concentrations. The main causes for the high production of ROS are environmental stresses such as drought and salinity [70]. In order to reduce the damaging effects of ROS, plants produce antioxidants, which include glutathione, ascorbate and carotenoids and ROS-scavenging enzymes which include superoxide dismutase (SOD), peroxidase (POD), catalase (CAT) and ascorbate peroxidase (AP or APX) [40]. In little millet, the activity of SOD, POD and CAT were elevated under drought conditions to enable the plant cope with unfavourable ROS accumulation [40]. Similarly, the activity of AP and monodehydro-ascorbate reductase (MDAR) increased in *tef* plants treated with drought compared to control plants receiving normal watering [71].

4.3. Genes involved in drought tolerance

The sequence of the genome and transcriptome of plants provides information important to the understanding of the types of genes involved in the regulation of drought tolerance, particularly in plants with increased resistant to moisture scarcity. So far, the genome of foxtail millet [72, 73] and tef [3] has been sequenced.

Transcriptome sequencing of millets after exposure to moisture-deficit condition provides information on genes differentially regulated under exposure to abiotic stresses particularly to drought. A transcriptome-wide study of finger millet plants exposed to drought obtained 2824 genes that were differentially expressed under these conditions [74].

Genes known to be involved in drought response and/or tolerance of selected millets are presented in Table 5. Wang et al. [75] indicated that the overexpression of SiLEA14, a type of LEA gene from foxtail millet, increased the tolerance of *Arabidopsis* plants to salt and osmotic stress. Parvathi et al. [76] reported the induction of several genes when finger millet was exposed to drought. The up-regulated genes include metallothionein, farnesylated protein ATP6, Farnesyl pyrophosphate synthase and protein phosphatase 2A.

Gene name	Source of the gene Test organism (type)		Reference
SiLEA	Foxtail millet	Overexpression in foxtail millet and Arabidopsis increased drought tolerance	[75]
SiARDP	Foxtail millet	Overexpression in foxtail millet and Arabidopsis increased drought tolerance	[83]
EcDehydrin7	Finger millet	Overexpression of EcDehydrin7	[80]
Ec-apx1	Finger millet	Expression increased under drought	[82]
Mt1D	bacteria	Finger millet expressing mt1D had better osmotic adjustment and chlorophyll retention under drought	[81]
Metallothionein,	Finger millet	Induced under drought	[76]
Farnesylated protein ATP6	Finger millet	Induced under drought	[76]
Farnesyl pyrophosphate synthase	Finger millet	Induced under drought	[76]
Protein phosphatase 2A	Finger millet	Induced under drought	[76]
RISBZ4	Finger millet	Induced under drought	[76]
β-carbonic anhydrase (PgCA)	Pearl millet	Up-regulated when exposed to drought	[79]

Table 5. Differentially regulated drought-related genes in millets.

Traits associated with drought tolerance were investigated using a genome scan and association mapping methods [77, 78]. A single gene known as β-carbonic anhydrase (PgCA) was

consistently up-regulated in pearl millet exposed to multiple abiotic stresses including drought, salinity and heat [79]. Hence, this particular gene is useful in adapting the plant to diverse abiotic stresses. Other genes known to be involved in drought response or tolerance in millets were EcDehydrin 7 [80], mt1D [81] and Ec-apx1 [82] from finger millet, and SiARDP [83] from wild foxtail millet.

Although not yet reported for millets, the suppression of two genes, namely, SAL1 and ERA1, increased the drought tolerance of the model plant *Arabidopsis thaliana* [84, 85]. The *era1* mutants develop tolerance to drought through a mechanism involving closing of the stomata [85].

5. Breeding millets for extreme drought tolerance

5.1. Germplasm acquisition and utilization

National and international efforts have been made to collect and maintain landraces of various millets types. The recent review by Goron and Naizanda [6] indicates the institutions involved in the preservation efforts and the amount of germplasm available at each institution. In general, India and China dominate the collections of millets. While institutions in India maintain 67% of the total of 33650 finger millet accessions, a single institution in China called the Chinese National Gene Bank preserves 61.2% of the total of 43,580 foxtail collections. Similarly, in the Ethiopian Institute of Biodiversity (EIB), over 5000 tef landraces collected from various tef-growing regions in the country are available [86]. Although these germplasm collections might not be exhaustive, they can play a key role in improving the productivity of respective crops. Further, large-scale expeditions need to be made for other millets in order to fully survey and bank the existing diversity in millets.

5.2. Breeding for drought tolerance

Breeding for drought tolerance is the major objective of many crop-breeding programmes due to the widespread prevalence of the moisture-deficit problem in global agriculture. A number of crops with drought tolerance have been developed. There are two options for the management of crops in water-limiting environments: the genetic and agronomic [87]. The genetic approach requires robust and reproducible screening methods for the identification of traits of drought tolerance in germplasm and breeding materials, and incorporation of the same into high-yielding varieties using conventional and biotechnological tools.

Crop breeding has relied for many years on conventional and ancient techniques such as selection and hybridization. Mutation breeding, the process of using chemicals or radiation to generate mutant plants with desirable traits, has also been used for several decades and has been a key in the release of over 2000 crop varieties to the farming community among which drought-tolerant cultivars are included [88]. Crop improvement techniques that apply modern genetic and omics (genomics, transcriptomics, proteomics and metabolomics) tools include the following: (i) *marker-assisted selection* (MAS) which refers to the utilization of molecular markers located near genes of interest to breed for traits that are difficult to observe, (ii) *TILLING* (targeting induced local lesions in genomes) [89] or *EcoTILLING* [90], the high-

throughput and non-transgenic techniques which rapidly detect point mutations in mutagenized populations, and (iii) *Gene* targeting that relies on the following three tools to increase the efficiency of gene targeting: *zinc-finger nucleases* [91, 92], *TALEN* (transcription activator-like effector nuclease) [93] and *CRISPR/Cas* (clustered regularly interspaced short palindromic repeats)/(CRISPR associated), type II prokaryotic adaptive immune system [94, 95].

5.3. Improved crop management

The wise use of crop management practices which include the time of planting, frequency of tillage and the rate and time of fertilizer application is important particularly in the semi-arid regions where moisture is scarce. Flexibility to change from late maturing crops to early maturing crops when the rainfall arrives late in the season is important. In the central semi-arid regions of Ethiopia farmers start their season by planting sorghum in April. When sorghum fails due to late arrival of rain, they sow wheat in June. However, if the rain is still late or not enough for wheat plant establishment, farmers sow tef in July or early August as the last option. Compared to sorghum and wheat, tef requires less moisture and matures early.

Suggestions have been earlier given on the type of technologies to be adopted in the semi-arid regions of Southern Africa [96] and West Africa [97]. According to Mir and colleagues, these technologies should include genomics, physiology and breeding [98].

5.4. Agricultural inputs and insurance

Access to agricultural inputs such as improved seeds, fertilizer and chemicals as well as credit and markets is important for farmers. In semi-arid areas where millets are dominantly cultivated, the amount and pattern of rainfall is erratic. Due to this, an insurance system known as Weather Index Drought Insurance has been implemented for the last decade in several African countries including Niger [99], Ghana [100], Kenya [101] and Burkina Faso [102] as well as India [103]. The successful insurance organization called 'Kilimo Salama' which was initially established by Syngenta Foundation for Sustainable Agriculture (SFSA) and implemented in several East African countries has been recently transferred to the Agriculture and Climate Risk Enterprise Ltd. (ACRE) [104, 105].

5.5. Partnership in research and development

Collaborations among national and international institutions are required in both research and development, in order first to develop improved millet cultivars and later to disseminate them to the farming community. Among the institutions with a global mandate to improve millets, ICRISAT (International Crops Research Institute for Semi-Arid Tropics) has recently added tef to the list of its mandate crops [106]. With its headquarters in Patancheru, India and regional offices in Nairobi (Kenya) and Bamako (Mali), it has been focusing on the improvement of diverse millets. The centre is among the 15 international agricultural research centers that belong to the CGIAR (Consultative Group for International Agricultural Research), the global partnership that unites organizations engaged in research for food security. Hence, the research and development of tef, a vital crop in the Horn of Africa that feeds over 50 million people in Ethiopia alone, will receive a global partnership towards its improvement and

development. In general, suggestions given to the improvement of understudied or orphan crops [107, 108] could also be applied to the research and development of millets.

6. Conclusions

Millets play a significant role in the livelihood of the population of developing world especially due to their enormous contribution to the food security of these countries. However, these crops have not been sufficiently studied and hence have been named orphan crops. Both conventional and modern improvement techniques have not yet been adequately implemented. It is believed that the changing climate will have significant effects on the types of crops cultivated in the next century. Currently, widely cultivated crops that provide the daily diet for many (such as wheat) might not be extensively cultivated in the future due to environmental stresses, especially the increase in global temperature. Millets might provide alternative climate-smart crops, as their adaptations to challenging environment are better than the current major crops of the world. Enhancing the productivity of millets requires concentered efforts of breeders, agronomists, policy makers and donors at both individual and institutional capacities.

7. Abbreviations

ABA; Absciscic acid

ACRE; Agriculture and Climate Risk Enterprise Ltd

AP or APX; Ascorbate peroxidase

CAT; Catalase

CGIAR; Consultative Group for International Agricultural Research

CSA; Central Statistical Agency (Ethiopia)

Ec-apx1; Ascorbate peroxidase

EIB; Ethiopian Institute of Biodiversity

FAO; Food and Agriculture Organization of the United Nations

FAOSTAT; Food and Agriculture Organization Statistics

GR; Glutathione reductase

ICRISAT; International Crops Research Institute for Semi-Arid Tropics

LEA; Late embryogenesis abundant

MDAR; Monodehydro-ascorbate reductase

Mt1D;; Mannitol dehydrogenase

PgCA; β -carbonic anhydrase

POD; Peroxidase

PVC; Polyvinylchloride

ROS; Reactive oxygen species

SFSA; Syngenta Foundation for Sustainable Agriculture

SiARDP; *Setaria italica* ABA-responsive DREB-binding protein

SiLEA14; *Setaria italica* late embryogenesis abundant 14

SOD; Superoxide dismutase

UN; United Nations

WRSI; Water Requirement Satisfaction Index.

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Author details

Zerihun Tadele^{1,2*}

Address all correspondence to: zerihun.tadele@ips.unibe.ch

1 Institute of Plant Sciences, University of Bern, Bern, Switzerland

2 Addis Ababa University, Institute of Biotechnology, Addis Ababa, Ethiopia

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