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Review

Impact of Drought on Maize Yield and Exploration of *In-Situ* Maize Crop Genetic Resources for Drought Tolerance.

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Abstract: To meet an ever global population's food demand, crop yields must be sustained and increased. Drought, which is getting harsher as a result of global warming, is largely impeding the agricultural productivity. Maize is widely used as food and animal feed in many regions of the world, but its yields are largely effected by drought and heat stress. Historical data on climate change predicts that drought and heat stress becoming major threat for maize cultivation in coming years, which will have huge impact on food security of the world especially in Africa and Asia. Thus there is an immense necessary to develop drought tolerant and climate resilient maize to feed the predicted population of the world. Availability and accessibility of crop genetic resources plays a huge role in development of drought-tolerant maize cultivars. A huge genetic resources of maize, including its landraces and crop wild relatives (CWR) have been reported naturally and many of them have stored in National and International gene banks globally. Conventional breeding methods have been tremendously increased maize yields, but these methods frequently fall short of achieving the demand for improved drought stress resistance. In this article, we have briefly discussed about impact of climate variability on crop production, maize yield losses due to drought, drought tolerance in maize landraces and CWR, and origin and evolution of Mexican landraces. This information may help in utilization of these potential resources in various pre-breeding programs.

Keywords: Maize; drought; landrace; climate-change; crop genetic resources

Background

After rice and wheat, maize (*Zea mays* spp. Mays) is the third most important crop in the world (Sandhu et al. 2007). Maize being originated in Mexico (Mesoamerica) and is the only cultivated species in its genus. Based on ancestry evidence maize descended directly from *Z. mays* ssp. Parviglumis (Balsas teosinte) (Doebley et al., 1990; Matsuoka et al., 2002). Molecular dating reveals that Balsas teosinte and maize diverged about 9000 years ago, which coincidences with archaeological dating (Piperno and Flannery 2001).

Maize is usually grown in tropical and temperate environments. The total maize harvested area and production increased by 86.8% and 460% from 1961 to 2019 in the world due to its high demand and divergent uses (Figure 1a) (FAO 2021). In Africa, it is most extensively cultivated and is a staple food for around half of Africa's population (Day et al. 2017). The global consumption pattern of maize is versatile; 61% of total production goes for feed, 17% for food, and 22% for industrial purposes (ICAR-IIMR 2021) (Figure

1b). The conversion ratio (the efficiency of converting feed into desired output) of the maize grains to produce meat, milk, and eggs is also higher than that of other grains (Lopez Pereira 1992). Further, nearly 3,500 products are derived from maize (FICCI 2018), including corn oil, ethanol, starch, and corn syrup.

Predicted population growth and the rapid shifting for meat intensive diets could double the human food demand by 2050 (Tilman et al. 2011). Maize is being extensively used as animal and poultry feed in China and India, thus increase in meat intensive diets in these highly populated countries could complementarily increases the demand for maize (Shiferaw et al. 2011) (Figure 1c & 1d). Hence a higher demand for maize may be expected in coming future. However, climate change seriously threatening agricultural production and yield stability in many parts of the world (Ray et al., 2015 and Summary of policymakers, IPCC, 2019). It has been discovered that rising temperatures in the summer diminish water availability for crops due to drying out of the air and soil, and also increase pest and disease incidence due to climate change (IPCC 2013). In farmer's fields, the two most important and frequently occurring abiotic stresses are drought stress (DS) and heat stress (HS) (Nelimor et al. 2020). Analysis of data published in peer-reviewed articles from 1980 to 2015, predicted that under 40 % soil water reduction, maize yield was reduced by 39 %, and also showed that maize was more drought-sensitive than wheat, especially during the reproductive phase (Daryanto et al. 2016). More information on effect of climate change and drought on crops with particular focus on maize was given in sections 2 and 3.

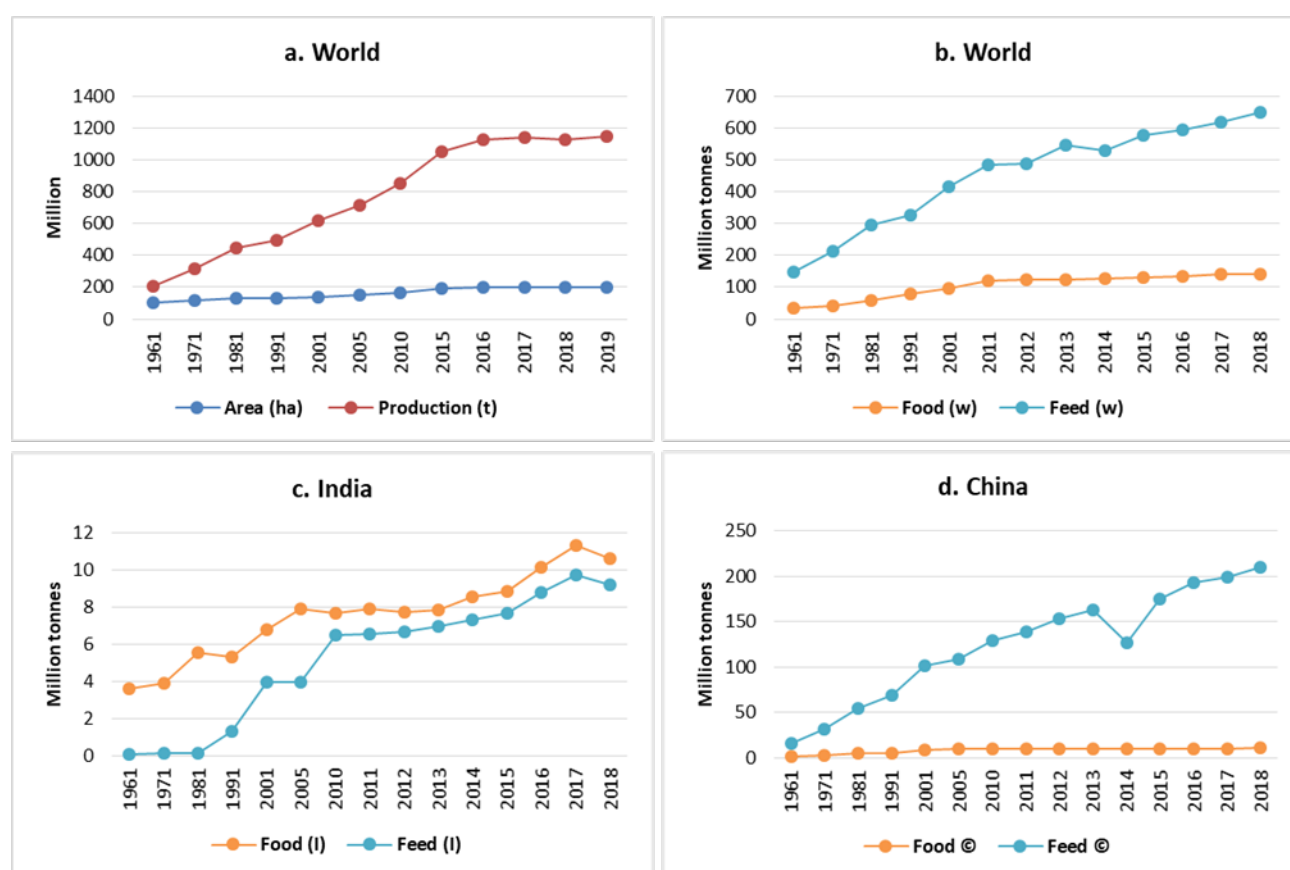


Figure 1: Global area, production and demand of maize. Source: (FAO 2021). a. World trend of maize area (million ha.) and production (million tonnes) from 1961-2019 (stagnation from 2015-2019), b. World trend of maize utilization as food and feed from 1961-2018, c. Trend of maize utilization as food and feed in India from 1961-2018. d. Trend of maize utilization as food and feed in China from 1961-2018.

Therefore, the development of new maize cultivars that are better suited to the changing climate is essential for the global food security (Burke et al. 2009). Various strategies have been deployed to develop climate-resilient cultivars including genetic modifications and traditional breeding, but it's noteworthy that traditional breeding has given greater success in the past (Burke et al. 2009). However, the success of traditional breeding has been supported by the accessibility and use of diverse crop genetic resources (landraces or crop wild relatives) that contain the traits for tolerance to drought, heat, or a specific pest or disease. Crop genetic resources are vital for adapting to climate change in agriculture since they are the primary source of new alleles for different crop stress-tolerating traits (FAO 2015a). This review provides brief information about impact of climate change on agricultural production, maize yield losses due to drought, natural crop genetic resources of maize available in the gene pool for drought tolerance and evolution of Mexican landraces.

Impact of climate variability on crop production

Climate change poses great threats to humanity and has far-reaching implications for the crop, environmental, and fisheries production (Global Commission on Adaptation, 2019; Wollenberg et al., 2016). Climate change destabilizes availability, access, utilization, and stability of the four pillars of food security (FAO 2015b). Moreover it has been forecasted that by 2050, the world's population will require 70% more food than it does now (FAO 2009). On the other hand, due to the indiscriminate use of natural resources by the exploding population (predicted to exceed 9 billion in 2050), water tables and water supplies continue to shrink worldwide. Over 70% of the freshwater in the world is used by agriculture, although peoples drink only 1 to 2 litres a day, while 2,000 to 3,000 litres is required to produce the food and meat we consume in a typical day (Edmeades 2013). Hence, expanding agriculture and livestock farming will significantly impact water table and shortage for crop production. Many of these impacts on crop production are already measurable, and adaptation actions to reduce risks are urgent (Wollenberg et al. 2016).

Extreme drought and floods, including monsoon and El Nino events (produce both droughts and floods) will become more common in future, and the areas vulnerable to severe droughts and floods may rise by 15-44% by 2050 (Global Commission on Adaptation 2019). Further, according to current climate estimates, extreme heat events are also expected to become more frequent and severe in the future, (Lesk et al. 2016). It's also projected that climate change would increase cereal prices by 1–29% by 2050, which may directly affect the consumer's purchasing power (Mbow et al. 2019). Since 1964-2007, droughts and extreme heat have reduced national cereal production by an average of 9–10 %, and the estimated production loss due to droughts and extreme heat was 1820 million tonnes and 1190 million tonnes respectively (Lesk et al. 2016). Furthermore, globally the average annual economic losses in agricultural production due to drought have exceeded USD 6 billion and are increasing (Wei et al. 2019).

Maize yield loss due to Drought

Maize productivity has been significantly altered by many biotic and abiotic stress (Assefa and Ayalew 2019). Drought and heat stress disrupt maize plants, and it induces stomatal closure, leaf firing, and tassel blasting, which directly damages the chloroplasts (Cicchino et al., 2011; Zaidi et al., 2016). Drought during flowering results in delayed silking and increases Anthesis Silking Interval (ASI) length (Bolaños and Edmeades 1996), hence due to lack of synchrony between silk emergence and anthesis (pollen shed), a decline in sexual fertilization and kernel set is observed (Westgate & Bassetti, 1990; Edmeades et al., 1993). Further, ASI is also can be used to estimate drought-induced yield reductions in maize (Edmeades 2013). As predicted by global climate models, droughts are expected to worsen and become more widespread in the major wheat and maize breadbaskets in the next decades due to climate change (Dai, 2013 and Trenberth et al.,

2015) Around 40 % of Africa's maize-growing area experiences occasional drought stress, resulting in yield losses of 10–25 %, while frequent droughts were observed in 25 % of the maize area resulting in losses up to 50% (Fisher et al. 2015).

During 1983-2009, droughts reduced yield in 124 million hectares of maize cultivating area and the global average of yield loss per drought was around 0.24 t/ha (Kim et al. 2019). It has been observed that over the last 50 years (1958–2007), drought has been correlated to an average of 13% of the variability in the United States's maize and soybean yields (Zipper et al. 2016). Moreover much of the consumed food in developing countries come from rainfed agriculture (95% of farmed land in Sub-Saharan Africa; 75% in the Near Eastern region and North Africa; 90% in Latin America; 65% in East Asia and 60% in South Asia), but water productivity, or "the amount of crop produced per drop," is known to be low in these rainfed areas (IWMI 2010). Approximately 160 million hectares of maize are grown in rainfed conditions around the world (Edmeades 2013). Additionally, maize is an important food and feed crop in these areas. Therefore a mere variation in yield due to various abiotic and biotic stress may lead many people to starvation, especially in Africa and Asia (Simtowe et al. 2019).

Maize Landraces and utilization for drought tolerance

Accessing and exploiting locally adapted varieties and landraces is very much needed under current climate change, landraces often guarantee higher services under less-than-ideal farming conditions and are extremely resistant to adverse environmental conditions (Ficiciyan et al. 2018). In Mexico, tremendous diversity and environmental adaptation of maize has been reported (Ruiz Corral et al. 2008). Sanchez et al., (2000) used isozyme and morphological analyses to estimate the genetic diversity of 59 Mexican maize landraces in 209 accessions and found a very tremendous level of variation both among and within the races. However, almost 65 % of the alleles discovered in these accessions were uncommon, with frequencies of less than 0.01. Wellhausen et al., (1952) conducted the first work on the systematics and taxonomy of Mexican maize landraces and classified them into 4 groups (Table 1 and Figure 2): 1) Ancient Indigenous, 2) Pre-Columbian Exotic, 3) Prehistoric Mestizos, 4) Modern Incipient and Poorly defined races. But Sanchez & Goodman, (1992) classified Mexican landraces after revisiting Wellhausen and Coworkers classification and divided 49 Mexican landraces based on morphological characters and cluster analysis into 3 major groups.

Table 1: Classification of Mexican landraces and their characteristics (Wellhausen et al. 1952).

Landrace/Race	Special traits	Elevation
I. Ancient Indigenous Races (AIR) (originated from primitive pod corn types)		
Palomero Toluqueno	Early maturing and highly resistant to maize rust race (<i>Puccinia sorghi</i>)	2200m-2800m
Arrocillo Amarillo		1600m-2000m
Chapalote	Early maturing & highly susceptible to rust	lower elevation
Nal-Tel	Early maturing, drought escaping and adopted to soils with less nitrogen.	lower elevation
II. Pre-columbian exotic races		
Cacahuacintle	Early maturing and highly resistant to rust races	
Harinoso de ocho	Best adapted for dry tropics	100m
Oloton	Highly resistant to rust	2000m-2400m
Maiz Dulce	Early maturing,	1000m-1500m
III. Pre-historic Mestizos		
Conico	Very early	2200m-2800m
Reventador		0-1500m
Tabloncillo	Early maturing	0-1500m
Tehua	Very tall and extremely late maturing	600-1000m
Tepecintle		0-600m
Comiteco	Late maturing and large ears	1100m-1500m
Jala	Very tall and late	1000m
Zapalote Chico	Very short, very early maturing, short tassel and adopted to low rainfall area,	100m
Zapalote Grande	Highly susceptible to rust,	100m-600m

Pepitilla		1000m-1700m
Olotillo	Tall and late maturing	
Tuxpeno	Tall and very late maturing	0-500m
Vandeno	Adopted to drier areas of the pacific coastal plains	0-500m
IV. Modern Incipient Races		
Chalqueno	Very tall (2-5 m)	1800m-2300m
Celaya	Productive race	1200m-1800m
Conico Norteno	Short and early maturing	
Bolita	Early maturing	900m-1500m
V. Poorly defined races		
Conejo	Very early in maturity (tres mezino), matures in 3 months and short stature	200m-350 m
Mushito	Very productive race	2400m
Complejo serrano de Jalisco	Very resistant to frost and adopted to high mountains	
Zamorano Amarillo	Very productive race	1500m
Onaveno		
Dulcillo del noroeste	Adopted to low land dry tropics	

Origin and evolution of Mexican landraces

According to Wellhausen et al., (1952) four pre-Columbian exotic maize races: Cacaahuacintle (floury), Harinoso de Ocho (floury), Olotón (flint) and Maíz Dulce were re-introduced from central and South America to Mexico during pre-historic times. These races hybridized with ancient indigenous races and local teosinte to give thirteen prehistoric mestizos (mixed race, especially one having Spanish and indigenous descent), and hybridization between these thirteen mestizos resulted in the creation of four current incipient maize varieties.

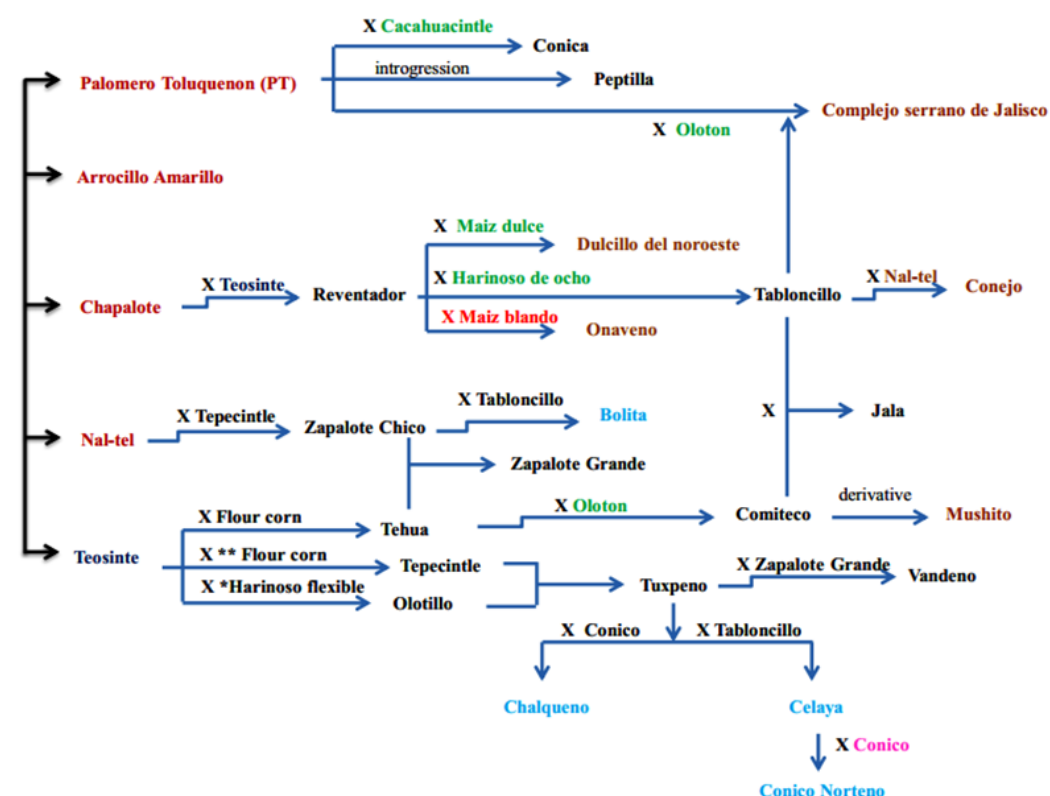


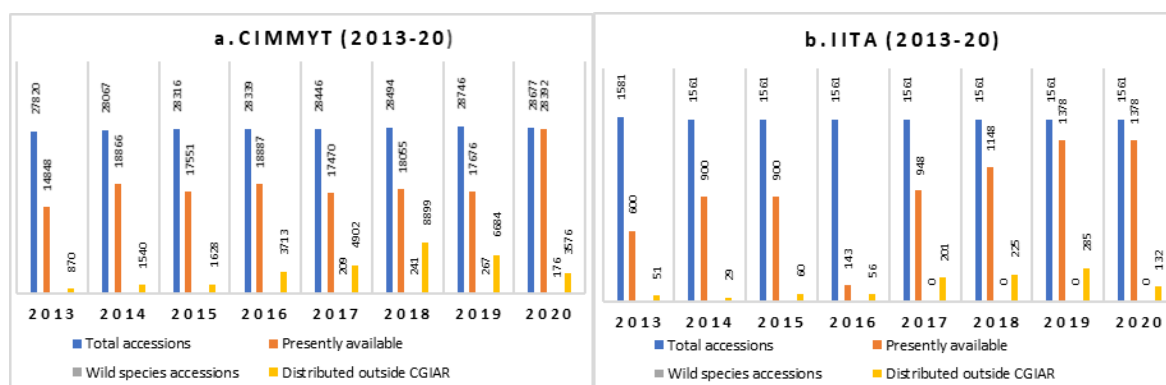
Fig. 2: Origin and evolution of Mexican landraces. Source: (Wellhausen et al. 1952). Palomero toluquenon (PT) crossed with Cacaahuacintle to give Conico, while Pepitilla is derivative of PT. Races Complejo serrano de Jalisco is a product of inter-hybridisation of 3 races PT, Oloton and Tabloncillo. Chapalote crossed with teosinte to give Reventador, which intern crossed with Maiz dulce, Harinoso de ocho and Maiz blanco to give rise to Dulcillo del noroeste, Tabloncillo and Onaveno respectively. Conejo found to be product of Nal tel and Tabloncillo. Nal tel crossed with Tepecintle to give rise to Zapalote chico, which intern crossed with Tabloncillo to give Bolita. Teosinte crossed with flour corn, another flour corn (may be Harinoso de guatt) to give rise to Tehua and Tepecintle

respectively. Harinoso flexible crossed with teosinte (*Zea luxurians*) to give Olotillo. Tehua crossed with Oloton to give Comiteco, and Mushito derived from Comiteco. Jala is derived from Comiteco and Tabloncillo, while Tuxpeno is derived from Tepecintle and Olotillo. Tuxpeno crossed with Zapalote grande, Conico, Tabloncillo to give rise to Vandeno, Chalqueno and Celaya respectively. Celaya intern crossed with Conico to give Conico norteno.

Drought tolerance in maize landraces and crop wild relatives (CWR).

It has been observed that landraces of maize demonstrate various traits, such as early maturation, drought tolerance (Table 2 and Figure 4) and disease resistance, as well as good cooking and eating qualities, which make them key genetic sources for local adaptation and sustainability traits (Mwololo 2010). Plants during evolution have developed a different developmental and metabolic mechanisms for efficient water utilization during both vegetative and reproductive growth (Parry et al. 2005). Landraces growing in semi-arid highland regions of Mexico were discovered to be relatively tolerant to drought (Eagles and Lothrop 1994). A huge amount of maize accessions including landraces and wild species are available in gene banks of International Maize and Wheat Improvement center (CIMMYT) and International Institute of Tropical Agriculture (IITA) (Figure 3).

In the above classification (Table 1), many landraces were found to have traits like early maturity, adaptation to drier conditions, and resistant to diseases. Early maturity is the best drought escape mechanism developed by plants. Landraces like Palomero Toluqueno, Chapalote, Nal-tel, Cacahuacintle, Maiz Dulce, Tabloncillo, Conico, Conico Norteno, Bolita, Conejo were reported by Wellhausen et al., (1952) to be early maturing and landrace Conejo reported to mature in 3 months (tres mezino), while landraces Vandeno, Harinoso de Ocho and Dulcillo del Noroeste were being adopted for dry and low rainfall conditions. Race Tuxpeno domesticated in the Oaxaca-Chiapas region (Kato 1988) with large variation, which has been extensively used in various maize improvement programs. It's derivative Tuxpeno Sequia is an early maturing and found to be drought-tolerant (Prasanna 2012). Race Bolita is described as drought tolerant with good tortilla-making properties (Prasanna 2012), and Olotillo an important local landrace performs well in poor soils (Benz 1987). Mexican maize landraces viz., La Posta Sequia, Cónica, Cónica Norteña, Bolita, Breve de Padilla, Nal Tel, Tuxpeno were found to be drought-tolerant (Prasanna 2012). International Maize and Wheat Improvement Center (CIMMYT) evaluated 600 landraces in 2014 and 2015 in both irrigated and drought stress conditions over multiple sites and observed that 52 landraces derived from Cristalino Colorado, Tuxpeño Norteño, Dentado Blanco, Tuxpeño, Dentado Blanco, Tabloncillo Perla, Onaveño, Tabloncillo were found to be drought tolerant, which can be available for distribution from the CIMMYT Germplasm Bank (CIMMYT 2021).



Source: CGIAR Gene bank Platform (<https://www.genebanks.org/genebanks/>).

Fig. 3. Crop genetic resources available in two Consultative Group on International Agricultural Research (CGIAR) maize gene banks from 2013-20. a. International Maize and Wheat Improvement center (CIMMYT); b. International Institute of Tropical Agriculture (IITA)

Andjelkovic et al. (2014) found that Serbian maize mini-core landraces L25, L14, L1, and L3 were seem to be drought-tolerant and showed a higher stress tolerance index. Nelimor et al., (2019) evaluated landrace accession from Burkina Faso, Ghana, and Togo for drought, heat, and combined drought and heat stress, and found landrace GH-3505 was highly tolerant to drought with a higher base index (used to choose the best and worst performing genotypes under stress), while landraces GH-4859 and TZm-1353 were tolerant to all three stresses. In the Serbian Maize Research Institute gene bank accessions, more than 50 genotypes were found to be drought-tolerant based on stay-green traits and total appearance (Babic et al., 2011). Further, drought screening of 78 landrace populations from southern Europe and temperate regions revealed that landraces from the dry areas were less vulnerable to water stress and had limited grain production, but a few of them showed very high yield under water stress too (Gouesnard et al. 2016).

Table 2: Various drought tolerant landraces and CWR's of maize.

Landrace/ CWR	Remarks	Reference.
Tuxpeno Sequia.	Early maturing	Prasanna, 2012
Race Bolita	---	Prasanna, 2012
La Posta Sequia, Cónica, Cónica- Norteña, Bolita, Breve de Padilla, Nal- Tel, Tuxpeno	---	Prasanna, 2012
Cajete Criollo & Michoacan 21	Latency trait	Rosa et al., 1964 Kanashiro et al., 2009
L25, L14, L1, and L3	High stress tolerance index	Andjelkovic et al., 2014
GH-3505	Higher base index	Nelimor et al., 2019
GH-4859 and TZm-1353	Tolerant to drought, heat and combined stress	Nelimor et al., 2019
JigawaAccNo.4(Y), JigawaAccNo.11, KanoAccNo.10, KatsinaAccNo.3, YobeAccNo.2 & YobeAccNo.3(Y)		Meseka et al., 2013
Zea may, ssp. Mexicana	Drought escape mechanism (short vegetative growth period)	Gonzalez et al., 2018
<i>Tripsacum dactyloides</i> var. <i>dactyloides</i>	Stay green traits, Roots penetrate hard soil and clay pans	Clark et al., 1998 Gilker et al., 2002

Six droughts adapted landraces (JigawaAccNo.4(Y), JigawaAccNo.11, KanoAccNo.10, KatsinaAccNo.3, YobeAccNo.2 and YobeAccNo.3(Y)) introgressed via backcrossing to maize and the resulted populations performed better than recurrent parent and commercial hybrids in multi-location trials in Nigeria (Meseka et al. 2013). The top three BC₁F₂ populations with 25% genome of the landraces yielded more grains than recurrent parent and commercial hybrid, and drought stress reduced grain yields of the BC₁F₂ populations by 64% and recurrent parent by 71% (Meseka et al. 2013). A drought adaptation trait named as "latency" seen in Cajete Criollo and Michoacan 21, in them, vegetative stage and flowering slowed and delayed respectively under drought and as soon as soil moisture is restored a rapid drought recovery was observed (Palacios de la Rosa et al. 1964). Further, Cajete Criollo and Michoacan 21 displayed more dramatic changes in global gene expression under drought stress, which were associated with various physiological mechanisms of drought adaptation (Hayano-Kanashiro et al., 2009).

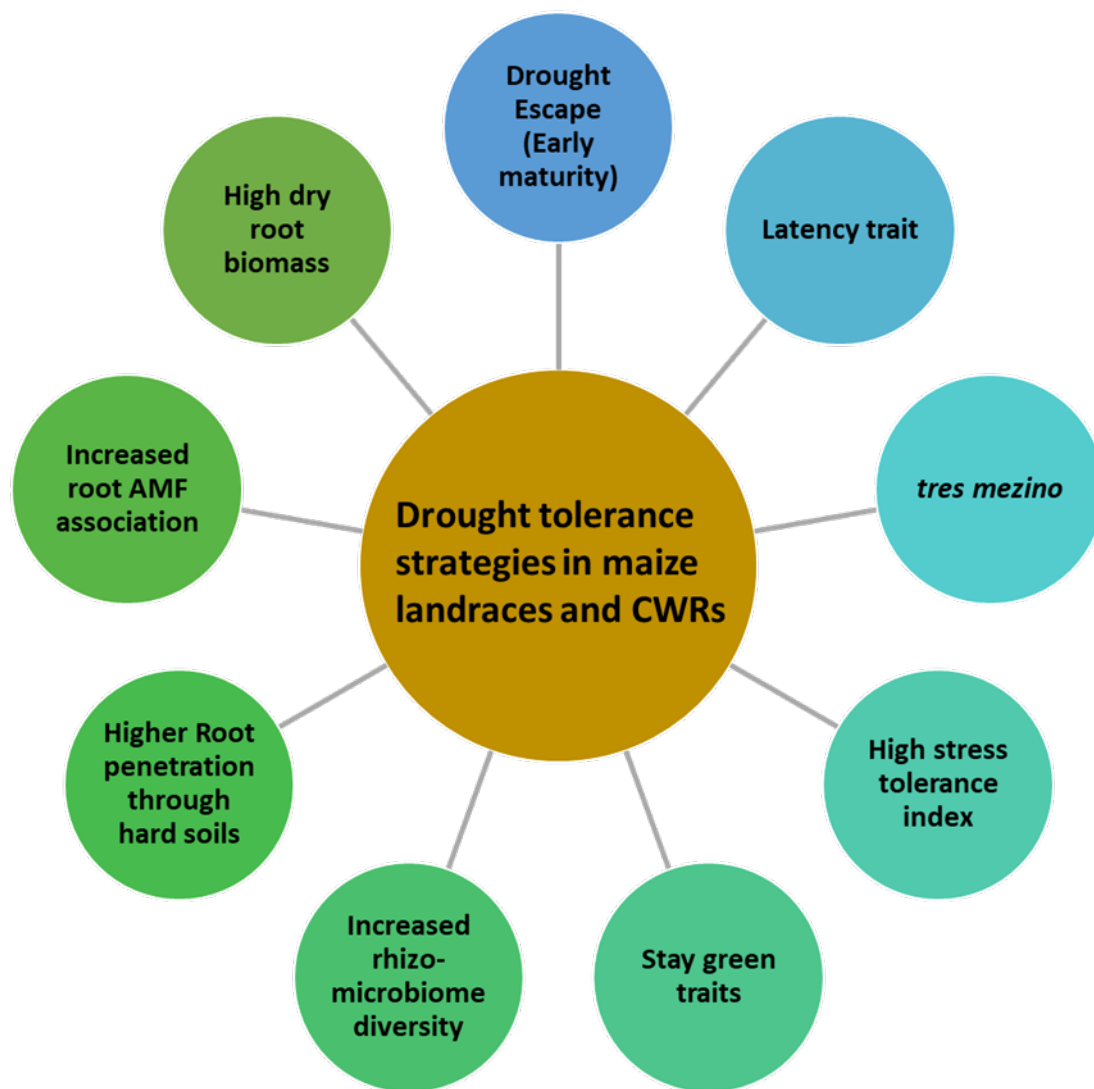


Figure 4: Drought tolerance strategies of maize landraces and CWRs.

Domestication and selection in maize have altered maize root architecture and exudates due to plant genetic changes which in turn influences the rhizo-microbiota, which is known to play very important role in various environmental stress tolerance (including drought) and physiological mechanisms (Pérez-Jaramillo et al. 2016; Valliere et al. 2020). In maize AMF was reported to help in alleviating drought stress through various morpho-physiological and biochemical processes (Boomsma and Vyn 2008). Two maize landraces of populace (Black and Yellow) subjected to low and medium soil Phosphorous (P) regime, showed higher colonization of native AMF and more P acquisition in the leaf than the hybrid maize, additionally Black landrace showed outstanding increase in root volume percentage and total dry mass of the plant under two P regimes (Sangabriel-Conde et al. 2014). Further this black landrace which showed highest AMF colonization and P acquisition was found to be associated with the highest number of AMF Operational Taxonomic Units (OTUs) (diversity) (Sangabriel-Conde et al. 2015). Thus landraces preserves more AMF diversity in the soil than the modern hybrid (Sangabriel-Conde et al. 2015). Szoboszlay et al. (2015) Evaluated *Zea mays* subsp. *parviglumis* (Balsas teosinte) and two maize cultivars for rhizosphere fungal and bacterial richness and found that shannon's and simpson diversity indices of bacterial Terminal restriction fragment length polymorphism (T-RFLP) of the 16S rRNA gene profiles were higher for teosinte than domesticated

maize. Moreover the balsas teosinte showed higher root dry biomass than shoot biomass, which is essential under drought and nutrient stress (Szoboszlay et al. 2015). Thus changes in root architecture due to continuous selection and breeding, could affect the rhizosphere microbe association and composition (Micallef et al. 2009).

In case of wild relatives of maize, the populations of *Zea mays* ssp. *Mexicana* are found to survive in the dry environment of Durango Valleys with drought escape mechanism (short vegetative growth period)(Gonzalez et al. 2018). Eastern gamagrass (*Tripsacum dactyloides* var. *dactyloides* (L.)) were often remained green during summer droughts, while other plants turn brown. Its roots are also observed to penetrate through hard claypans (Clark et al. 1998) and high soil strength layers (Gilker et al. 2002), which may help in adopting to dry environments. It also showed higher CO₂ exchange rate and high transpiration efficiency (10 mmol mol⁻¹) under optimum soil water conditions (Coyne and Bradford 1985).

Conclusion and Future aspects:

Droughts have becoming more frequent and severe, resulting in lower crop yields. Due to climate change and frequent droughts, maize yields and productivity are significantly un-stabilised, which may pose significant threat on global food and feed security, especially in Africa and Asia, where it is largely used as staple food and prominent feed to produce the meat. Moreover drought also exaggerate other abiotic and biotic stress like heat and insect pest. Thus developing drought-tolerant and climate resilient cultivars are of great necessity to sustain the income of farmers and global food security. Dynamic gene pool of maize, holds various primitive landraces and crop wild relatives which possess novel alleles and mechanisms to sustain under low soil water conditions, pest attack and climate extremities (Prasanna 2012; Singh et al. 2021). Utilisation of these vast genetic resources, available naturally and stored in gene banks could assist various pre-breeding programs directed towards developing climate resilient maize cultivars. However complexity of the drought tolerance trait and high genetic load of these resources may impede their efficient utilisation. But deployment of present biotechnological innovations and tools may overcome these obstacles. Further, physiological and molecular understandings of the drought tolerance mechanisms acting in these genetic resources could help in developing various markers for robust phenotyping for drought tolerance. However, these approaches need to be backed by contemporary omics tools in order to achieve their full potential.

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Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

GMS, GG and SS designed the draft, reviewed the literature and prepared preliminary draft; FZ, SRS, SSP, PSS and JX helped to structure and synthesize the review, and supervised for draft preparation; SS and VKM critically revised the draft.

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