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Conventional and Molecular Improvement of Maize for Drought Tolerance

Belay Garoma
Bako National maize research centre, Bako, Ethiopia
*Corresponding author: belaygaroma@gmail.com

Abstract
Maize is an important staple crop for food, feed, bioenergy and industrial products globally. Despite the importance of maize as a principal food crop in developing countries, drought is a major constraint that affects maize production, particularly in Sub-Saharan Africa, where maize is grown under rainfed conditions. Plant breeders have been striving to improve and develop drought-tolerant variety. Nevertheless, these efforts still cannot meet the demand for food security due to fast population growth and climatic change. Conventional maize breeding for drought tolerance follows diverse approach includes recurrent selection, backcrossing, pedigree breeding, and subsequently evaluating inbred lines and hybrids at optimum conditions, managed screening site and random stress across multiple environments. Molecular markers were used to select donor parents with drought-adaptive alleles and then integrated into elite maize lines to create a new population of drought-tolerant maize inbred lines and subsequently used to develop hybrids maize tolerance to drought stress.

Key words: Secondary traits, molecular markers, drought -adaptive alleles, maize

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1. Introduction

Maize (*Zea mays L.*) is a worldwide important staple crop for food, feed, bioenergy and industrial products. Despite the importance of maize as a principal food crop, particularly in developing countries, its average yield in Africa (2.02 t ha^{-1}) is still low as compared to the world average (5.58 t ha^{-1}) (FAOSTAT, 2021). A significant portion of this yield gap is attributable to biotic and abiotic stresses. Adverse environments such as drought, salt, and high temperatures can affect maize growth and cause considerable yield loss. Among all, drought is a major constraint that affects crop production across the world, particularly in sub-Saharan Africa, where maize is grown under rainfed conditions. It is estimated about 15% to 20% of maize grain yield is lost each year due to drought, and even such losses may increase further because of climate change-induced rising temperatures and fluctuations in rainfall (Thomson *et al*., 2005; Cairns *et al*., 2013). Furthermore, climate change can further intensify the frequency of drought and significantly reduce maize grain yields (Mulungu and Ng'ombe, 2019).

Drought affects at any maize growth stages. When drought occurred at the vegetative stage, it resulted in reduced leaf area, root spread, stem extension and metabolic activity. Also, it reduces the chlorophyll content and light interception, onward in low photosynthesis and subsequently reduced maize yield (Athar and Asharf, 2005). The fact that maize is more sensitive to drought at flowering or occurring between two weeks before and after the silking stage can cause significant yield loss of about 20% to 50% (Nielson, 2007), Figure 1. If drought is severe and critical at flowering and extends throughout grain filling, it may lead to the complete abortion of ears, and the crop may become barren, and/or ears may have fewer kernels, which is very correlated with grain yield (Rhoades and Bennett, 1990; Edmeades, 2013).

So far, plant breeders have been striving to improve and develop drought-tolerant crops. Nevertheless, these efforts still cannot meet the demand of food security due to fast population growth and climatic change. Thus, the objective of this paper was to review the states of maize breeding for drought conditions using conventional breeding and molecular markers.

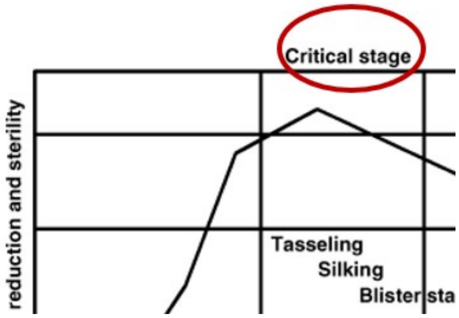

Figure 1. Drought stress at different stages of maize development (Rhoades and Bennett, 1990).

2. Plants response to drought stress

In an agricultural context, **drought** is a situation when the water availability of a plant is less than what is required to sustain its growth and development, or **drought** is a situation when there is inadequate moisture in the soil at a particular time to meet the needs of the plant. Plants use different mechanisms to cope with the drought. These strategies (mechanisms) include drought escape strategies, i.e., early flowering time before the onset of the drought season, and maturation, meaning that plants undergo the completion of their life cycle prior to the detrimental effect of drought (Deikman *et al*., 2011). For example, Melkasa maize breeders in Ethiopia evaluated and selected maize germplasm that can escape drought via early flowering. So far, Melkassa1, Melkassa1Q, Melkassa4 (OPV), and hybrid maize (MH130, MH140, MH141) have been released and commercialized in low-moisture stress areas that receive annual rainfall < 800 mm in Ethiopia. Thus, farmers in low-moisture and marginal areas are using such varieties. However, a yield penalty can occur when too early varieties. Drought avoidance is also another strategy when plants improve water use efficiency through closing stomata, leaf rolling, increasing the thickness of the leaf cuticle, or improving water uptake via developing the root system. Plants also adapt metabolism mechanisms to minimize water loss, such as osmatic adjustment through active accumulation of solutes in the cell, which helps for retention of water and limits turgor loss (Paillard *et al.,* 2003; Ribaut *et al*., 2009; Gowda *et al*., 2011). Traits like relative water, proline, and chlorophyll contents are also the most reliable parameters for drought tolerance in plants (Rahul *et al*., 2018). Drought escape and avoidance mechanisms are associated with morphological traits that can be exploited from diverse germplasm and selected at drought-prone areas.

3. Field management for drought stress

Testing environments should be taken into consideration in relation to rainfall distribution, soil properties, altitude, genotype × environment interaction and market demand. Evaluation of maize germplasm for drought tolerance should be carried out at optimum conditions under water stress during the rainy period using controlled irrigation, managed screening sites, and random stress. Water stress is induced during the flowering and grain filling growth stages, and its average yield under stress could be reduced by up to 30% relative to the un-stressed yield (Maazou *et al., 2016*). Similarly, maize germplasm is induced at flowering time, which means drought stress coincides with anthesis and silk emergence, named severe stress (Banziger *et al*., 2000), and onwards supplementary irrigation should be applied.

3.1. Importance of secondary traits under drought tolerance in maize breeding

Grain yield under stressful conditions is often the primary and complex trait for selection. Secondary traits such as anthesis-silking interval, ear per plant, leaf senescence, stay green, chlorophyll content, and other morphological traits that are associated with grain yield should be considered under drought stress conditions (Lafitte *et al*., 2003; Banziger *et al*., 2006). Also, secondary traits should be genetically correlated with yield, exhibit genetic variation, have a high level of heritability, and be simple to measure (Ribaut 2009). When drought coincided at anthesis silking interval, it affected embryonic development and early grain filling; yield loss estimated about 45% to 60% (Campos *et al*., 2006; Kumar *et al*., 2015). Furthermore, maize ovary abortion is greatest when drought is severed a few days before pollination, meaning that water deficiency around pollination increases the frequency of seed set abortion in maize due to a lack of photosynthate and to the distress of carbohydrate metabolism in ovaries (Zinselmeier *et al*., 1995). Banziger *et al.* (2006) reported that

90% decreased in yield as ASI increased from -0.4 to 10 days. On the other hand, the shorter ASI led to a positive association between ASI and grain yield and, indirectly, ear per plant and kernel per row selected. Monneveux *et al*. (2005) reported that ears per plant showed significant correlation with grain yield across drought (r = 0.96), low-N (r = 0.66) and optimum (r = 0.83) environmental conditions (Figure 2).

Delayed leaf senescence and high chlorophyll contents are also associated with the stay-green and key traits for drought tolerance. Stay green maize can retain the moisture and help better in photosynthesis during the grain filling stages (Lee and Tollenar, 2007). Thus, plants survive with the existing soil moisture and maximize their grain filling efficiency. Consequently, breeders select genotypes that are capable of converting the sources to sink rapidly. For example, leaf growth and ASI are the secondary traits that determine the source and sink strengths of maize via their relationships with light interception and yield, respectively. In addition, staying green and root architecture are the most important secondary traits to impart drought tolerance and indirectly contribute to yield (Nepolean *et al*., 2013). Thus, indirect selection through secondary traits that are associated with grain yield can improve the efficiency of maize breeding under drought conditions. Therefore, secondary traits are highly significant and associated with grain yield and should be considered for selection under drought stress in the maize breeding program.

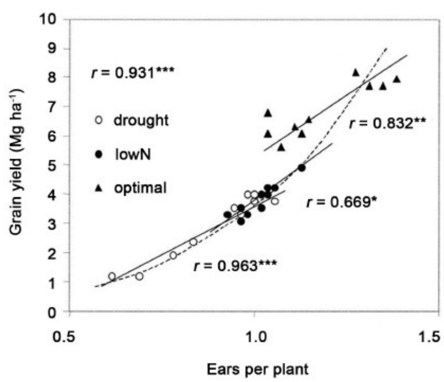

Figure 2. Correlation of ears with grain yield under drought, optimum and low-N

4. Breeding scheme

Maize breeding for drought tolerance is carried out by CGIAR; CIMMYT and IITA with the collaboration NARS in sub-Saharan Africa. At the beginning, intermediate and early-maturing stress-tolerant maize germplasm were tested in multiple countries in a wide range of environments and selected. Nearly two decades ago, the African Maize Stress (AMS) Project was launched with the collaboration IITA, CIMMYT and NARS in SSA to develop maize varieties and elite lines for drought tolerance (Menkir *et al., 2024).*

5. Broadening Gene Pool

The first worth of a maize breeding program is broadening the gene pool, classifying inbred lines into heterotic groups using reliable opposite testers and markers, exploiting their variation among advanced inbreds, and subsequently assessing combining abilities among inbred lines for yield, drought tolerance, disease resistance, and other desirable agronomic traits. Broadening is step-wise through the introgression of drought-tolerant parents that carry favorable alleles or genes and recycle them for target traits. Breeding for drought tolerance is a state of motion to be continued to introduce exotic maize inbred lines from different genetic backgrounds that having novel alleles of adaptive drought-tolerant lines and then introgressed into elite lines to broaden germplasm and diversify the genetic base within and opposite heterotic groups. Maazou *et al.* (2022) reported that tropical inbred lines were characterized into two heterotic groups using SNP markers, cluster analysis, testcross performance, and yield-based affinities. A similar study reported that heterotic grouping inbred lines fell into four groups, suggesting that each sub-group displayed the presence of substantial genetic diversity among these inbred lines, and this can maximize genetic variation for inbred line development and heterosis manifestation.

5.1. Conventional breeding for drought tolerance in maize

Maize breeding programs for drought tolerance follow diverse strategies such as recurrent selection, backcrossing, and pedigree breeding methods to exploit genetic variation while evaluating segregant population, fixed lines and hybrids under managed and across multi-environments at optimum and drought prone areas. The source of germplasm should be exhibited high allelic variation and diverse adapted parents that can promote drought tolerance (Reynolds and Tuberosa, 2008). The divers' sources include adapted elite lines developed from introgression, multi-parent populations and parental lines these carrying favorable alleles for drought tolerance that maximize genetic diversity within and opposite heterotic groups. Crossing within heterotic groups can start for inbred line development for target traits. For example: drought tolerance x drought tolerance for target traits; drought tolerance x heat tolerance, drought tolerance x low N tolerance, drought tolerance x disease resistance etc.

5.1.1. Performance of maize inbred lines and hybrids under managed and drought stress

The aim of maize breeding for drought tolerance is 1) to reduce the yield gap between optimum and stress conditions, 2) to advance the yield stability across stress conditions. This can be employed by evaluating diverse maize germplasm under drought stress and optimum conditions. indicating that several inbred lines populations and hybrids screened under managed drought tolerance and optimum at the flowering and grain filling stages. Several studies have reported on the evaluation of inbred lines for drought tolerance. Chandel *et al*. (2012) assessed maize inbred lines for ASI, plant height, leaf senescence, leaf rolling, and yield under limiting irrigation verses normal irrigation at knee height, flowering and grain filling. The performed inbred lines or families were selected based on high grain yields, short ASI, increased ears per plant, and reduced leaf senescence under managed drought stress were also assessed under watered conditions. Likewise, hundred maize inbred lines evaluated under contrasting soil moisture conditions, and among these fifteen inbred lines showed high tolerance to drought. Moreover, the tolerance inbred lines showed shorter ASI, a low canopy temperature, higher chlorophyll content and a comparatively higher grain yield when subjected to drought stress (Shadakshari and Shanthakumar, 2015). Likewise, eleven inbred lines evaluated under drought and heat over two years, and among these two inbred lines revealed that they had a relatively high-water content and improved damage to reproductive tissues under drought conditions (Chen *et al*., 2012). Also, Malook *et al*. (2016) reported that a high heritability was found for plant height, thousand kernel weight, grain rows per ear and grain yield per plant, in addition, the selected inbred lines showed high specific combing ability for yield under stress conditions. Several studies showed that physiological traits such as stomata conductance, chlorophyll content, transpiration rate, leaf water potential, and relative water content were used to improve breeding stress tolerance. For example, Dordas *et al*. (2018) reported a better association between physiological characteristics and grain yield under stress conditions for inbred lines than hybrids, and these traits are strongly helpful for the selection of adaptive parents. Similarly, a correlation of secondary traits with grain yield under stress conditions was conducted. Canopy temperature depression ($r = 0.61$) and chlorophyll present in sampled leaves ($r = 0.50$) showed positive correlation, while leaf rolling score ($r = -0.49^{**}$), leaf senescence score ($r = -0.57$) and anthesis silking interval ($r = -0.15$) showed negative correlation (Parajuli *et al.,* 2018). This means that increasing leaf roiling and subsequent leaf drying early and non-nicking of ASI result in decreasing grain yield.

After the evaluation of several inbred lines, promising lines were selected based on their tolerance. The selected F4 stages should be crossed at least by two opposite testers, and their crosses should be evaluated under managed drought tolerance for direct selection and evaluated in a broad array of environments in drought-prone areas. The hybrid maize that was selected under stress might be reduced to at least 50% of its yield potential (i.e., if yield under optimum conditions is around 7 t/ha, yield under stress is likely about 3.5 t/ha) (Banziger *et al.,* 2006). Forty drought-tolerance hybrids evaluated under well-watered drought and heat over three years and found a significant difference among hybrids for grain yield, and the yield showed a positive correlation with secondary traits (Meseka *et al*., 2018), and three hybrids produced a high grain yield under three conditions. Similarly, forty-nine maize hybrids that were developed via Line by test cross were evaluated under drought stress, low nitrogen, and optimum conditions and showed that the drought stress reduced grain yield and plant height. The authors also noticed that further maize improvement for grain yield is required under stress and optimum conditions (Ertiro *et al.,* 2017).

5.2. Molecular markers to dissect drought tolerance traits

Advanced genomics-assisted breeding techniques such as marker-assisted selection (MAS), marker-assisted backcrossing, and marker-assisted recurrent selection (MARS) are fast approaches and possibilities for drought tolerance improvement. Understanding the genetic and physiological basis of target traits is useful information during selection for drought tolerance. Quantitative trait locus (Quantitative traits locus, QTL) is included both phenotypic data (trait measurement) and genotype data using DNA markers that attempt to uncover the genetic basis of variation in traits (Chamarthi *et al*., 2011).

5.2.1. Identification of Quantitative Traits Locus associated with drought tolerance traits

Drought tolerance is a complex nature in quantitative trait that is controlled by several genes and affects genotype by environment interaction. Many QTLs that control morpho-physiological traits and grain yield under water-limited conditions have been identified in maize. For instance, several QTLs detected across six chromosomes for secondary traits such as ASI, ear per plant, stay green and plant height (Wange *et al*., 2012; Almeida *et al*., 2014), Figure 3. Out of the detected QTLs, 65% were identified under water stress, suggesting the significance of secondary traits for maize breeding under drought tolerance. The authors also reported that twenty-nine QTL were detected for ear per plant and 80 QTL for stay green (leaf senescence and chlorophyll content) in maize populations under both conditions. Also, Zhao *et al.* (2018) found 62 QTLs for major agronomic traits, and out of these, nine QTLs were detected for ASI and ear length. Out of these, 75% (52 QTLs) were detected under water-stressed conditions, suggesting a high possibility for maize improvement under stress conditions.

It was interesting that clustered QTLs were found on chromosome 3 that harbored QTL (hotspot region) for most morpho-physiological traits (Almeida *et al*., 2014). Similarly, co-located QTLs were found on chromosomes 1, 3, and 5 for ear height and ASI under both conditions (Yang *et al*., 2008; Ribaut *et al. 2009*). It is suggesting that the same gene for controlling different traits or loci has a pleiotropic effect that controls multiple traits. Similarly, Zhao *et al*. (2018) also identified 36 meta-QTLs across 26 populations under stress and watered conditions and several candidate genes were identified through fine mapping, suggesting that these inbred lines can use as introgression into elite lines for drought tolerance. Additionally, a cluster of QTLs was detected for plant height, TKW, and grain yield per plant, and these may be used to enhance maize drought tolerance under water-limited environments (*Chene et al.,* 2012).

The above results may suggest that molecular markers linked to secondary and desirable agronomic traits under stress enable the transfer of the donor parent into elite lines (Ribaut *et al.* 2002). Furthermore, molecular markers were used to select donor parents with drought-adaptive alleles and then integrated into elite maize lines to create a new population of drought-tolerant inbred lines. For example, Almeida *et al*. (2013) detected QTL in relation to GY with ASI and then introgressed into a drought-prone maize line, showing increased grain and lower ASI. Also, Bankole *et al.* (2017) reported that marker-assisted recurrent selection (MARS) helps to improve drought tolerance in population and yield gain per cycle and increase the frequencies of favorable alleles.

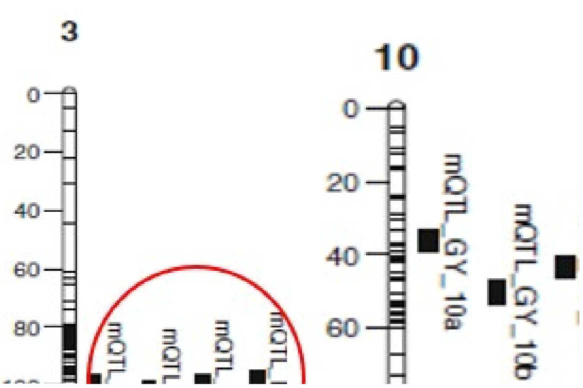

Figure 3. QTLs detected across chromosomes for ASI, ear per plant, stay green, plant height ear ratio under stress and water regime (Wange *et al*., 2012; Almeida *et al*., 2014)

6. Conclusion

Drought is a major constraint that affects maize production, particularly in Sub-Saharan Africa, where maize is grown under rainfed conditions. Plant breeders have been striving to improve and develop drought-tolerant variety through conventional and molecular breeding approach. The conventional method includes recurrent selection, backcrossing and pedigree breeding meanwhile considering secondary traits for selection under drought stress and optimum that are directly associated with grain yield. Furthermore, several QTLs regulating important morpho-physiological traits were identified, molecular markers developed, and used to select donor parents with drought-adaptive alleles, and then integrated into elite maize lines to create a new source population of drought-tolerant inbred lines and subsequently develop hybrid resilience to drought stress.

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