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Review Article

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Conventional and Molecular Improvement of Maize for Drought Tolerance: Research Review

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ABSTRACT
Maize (Zea mays L.) is an important staple crop for food, feed, and industry 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 crops. 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 a diverse approach that includes recurrent selection, backcrossing, pedigree breeding, and subsequently evaluating inbred lines and hybrids at optimum conditions, a 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 inbred lines.

Keywords: Secondary Traits, Molecular Markers, Drought Adaptive Alleles, Maize

Introduction

Maize (Zea mays L.) is a worldwide important staple crop for food, feed, and industry. 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) [1]. 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 that 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 [2,3]. Furthermore, climate change can further intensify the frequency of droughts and significantly reduce maize grain yields [4].

Drought affects at any growth maize 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 as well as light interception, resulting in low photosynthesis and subsequently reduced maize yield [5]. 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%, Figure 1 [6]. 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 [7,8].

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

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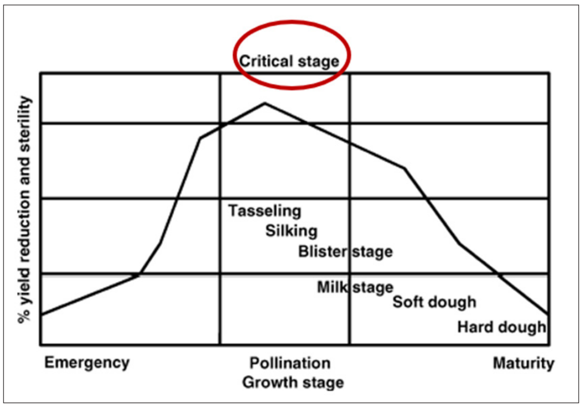

Figure 1: Drought stress at different stages of maize development [7].

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 [9]. For example, breeders evaluate and select maize germplasm that can escape drought via early flowering. However, a yield penalty can occur when too early. 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 [10-12]. Traits like relative water, proline, and chlorophyll contents are also the most reliable parameters for drought tolerance in plants [13]. Drought escape and avoidance mechanisms are associated with morphological traits that can be exploited from diverse germplasm and selected in drought-prone areas.

Field Management for Drought Stress

Selection and testing environments should be taken into consideration in relation to rainfall distribution, soil properties, altitude, and genotype × environment. 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 [14]. Similarly, maize germplasm is induced at flowering time, which means drought stress coincides with anthesis and silk emergence, named severe stress, and onwards supplementary irrigation should be applied [15].

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, era per plant, leaf senescence, staying green, chlorophyll content, and other morphological traits that are associated with grain yield should be considered under drought stress conditions [16,17]. Also, secondary traits should be genetically correlated with yield, exhibit genetic variation, have a high level of heritability, and be simple to measure [11]. When drought coincided at anthesis silking interval, it affected embryonic development and early grain filling, resulting in a resulting in a yield loss estimated at about 45% to 60% [18,19]. 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 [20]. Banziger et al. reported that 90% decreased in yield as ASI increased from -0.4 to 10 days [17]. On the other hand, the shorter ASI led to a positive association between ASI and grain yield and, indirectly, ears per plant and kernel per row selected. Monneveux et al. 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).

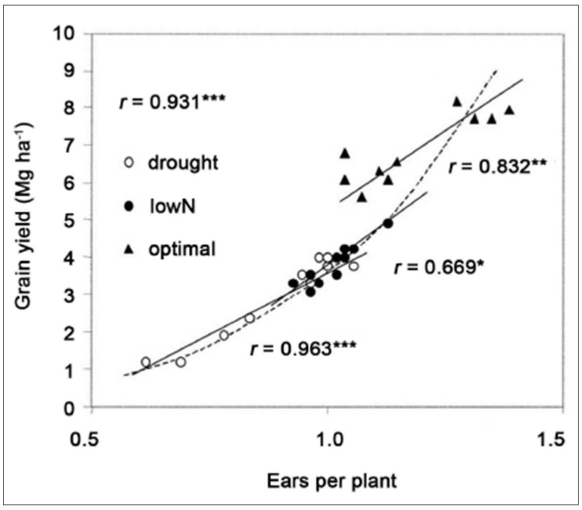

Figure 2: Correlation of ears with grain yield under drought, optimum and low-N.

Delayed leaf senescence and high chlorophyll contents are also associated with the stay-green and key traits for drought tolerance. Stay green, retain the moisture, and help better in photosynthesis during the grain filling stages [21]. 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 [22]. 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.

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 [23].

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 who 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 broaden the germplasm and diversify the genetic base to harness parents with novel alleles of adapted drought-tolerant lines within and opposite heterotic groups [24]. Maazou et al. 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.

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 inbred lines and hybrids under managed and multi-location drought stress. Identifying adaptive parents and crossing within heterotic groups for inbred line development and subsequently serious evaluation of the segregant population [25,26]. The source of germplasm should exhibit high allelic variation and be diverse, promoting drought tolerance. The divers' sources include adapted elite lines derived from introgression, multi-parent populations, parental lines carrying favorable alleles for drought tolerance, and other sources that maximize genetic diversity within and between heterotic groups. Crossing within heterotic groups would be started for inbred line development for targeting traits. For example: drought tolerance x drought tolerance for considering target traits; drought tolerance x low N tolerance; drought tolerance x disease resistance; and drought tolerance x susceptibility for inbred line development. Notice that the current trend of inbred line development in maize is through the pedigree method, modified single seed decent, back crossing, and double haploid.

Evaluation of Inbred Lines and Hybrids Under Managed and Drought Stress

The goal of maize breeding for drought tolerance is 1) to reduce the gap between yields in optimal and stressful conditions and 2) to improve yield stability for a range of stress conditions. This can be employed by evaluating a wide array of maize segregants under drought stress versus optimum conditions. This means that several segregant populations were 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. evaluated 190 maize inbred lines for different morphological parameters: ASI, plant height, leaf senescence, leaf rolling, and grain yield/plant under limiting irrigation vs, normal irrigation at different growth stages, viz., at knee height, grain filling, before flowering, and both at flowering and grain filling [27]. The selected inbred lines or families 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, one hundred maize inbred lines were evaluated under contrasting soil moisture conditions, and 15 inbred lines showed high tolerance to drought. Also, tolerance inbred lines showed shorter ASI, a low canopy temperature, a lower drought susceptibility index, higher chlorophyll content, and a comparatively higher grain yield when subjected to drought stress [28]. Similarly, eleven inbred lines were evaluated under drought and heat over two years, and two of the inbred lines revealed that they had a relatively high-water content, greatly maintained vegetative growth, and improved damage to reproductive tissues under drought conditions [27]. Likewise, Malook et al. reported that a high heritability and genetic advance were found for plant height, thousand kernel weight (TKW), grain rows per ear, and grain yield per plant, as well as a high specific combing ability, suggesting that some parental lines showed superior ability to develop higher yield maize hybrids under stress conditions. Most studies demonstrated 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. Dordas et al. 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 [29]. 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. 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 are 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) [17]. Forty drought-tolerance hybrids were 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, and three hybrids produced a high grain yield under three conditions [30]. Likewise, forty-nine maize hybrids that were developed via line testing 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 [31].

Development of early maize maturity through conventional breeding in moist areas was also conducted. The escaping strategy is the fact that plants accelerate their flowering time before the onset of the drought season. 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) 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. Similarly, Monneveux et al. evaluated CIMMYT maize populations under drought, low N, and optimal conditions and showed a yield gain per cycle and a significant increase in terms of ears per plant and the number of grains per ear.

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 secondary traits is useful information during selection for drought tolerance in crops. Quantitative trait locus (QTL) is linked to phenotypic data (trait measurement) and genotype data using molecular markers that attempt to explain the genetic basis of variation in traits [32].

Identification of Quantitative Traits Locus Associated with Drought Tolerance Traits

Drought tolerance is a complex quantitative trait in maize that is controlled by many genes and affects genotype-environment interaction. Secondary traits are expressed under drought tolerance, and their genetic basis is dissected using markers. Several QTLs that regulate morpho-physiological traits and grain yield under water-limited conditions have been identified in maize. For instance, several QTLs were detected across six chromosomes for ASI, ear per plant, stay green, plant height, ear ratio under stress, and water regime, Figure 3 [33]. Out of the detected QTLs, 65% were identified under water stress, suggesting the relevance of secondary traits for breeding under drought tolerance. The authors also reported that 29 QTL were detected for ear per plant and 80 QTL for stay green (leaf senescence and chlorophyll content) in three maize populations under both conditions. Similarly, several QTL were identified under both conditions for different traits and common QTLs shared [34]. Also, Zhao et al. found 62 QTLs for major agronomic traits, and out of these, nine QTLs were detected for ASI and ear length [35]. Out of these, 75% (52 QTLs) were detected under water-stressed conditions, suggesting a high possibility for maize improvement under stress conditions. Traits were located on different chromosomes under different conditions, suggesting that different genes influence different physiological processes that contribute tothe expression of different morphological traits under different conditions.

It was interesting that clustered QTLs were found on chromosome 3 that harbored QTL (hotspot region) for most morpho-physiological traits as well as the location of two important candidate genes and consequently useful for marker-assisted introgression for drought tolerance in tropical maize [33]. Similarly, co-located QTLs were found on chromosomes 1,3 and 5 for ear height and ASI [36]. It is suggesting that the same gene for controlling different traits or loci has a pleiotropic effect that controls multiple traits. Clustered QTLs were also detected for both stressed and watered conditions. Likewise, overlapped QTLs were found for leaf growth and ASI in inbred lines of maize under water stress conditions, suggesting that a high leaf elongation rate conferred a short ASI, indicating a high silk elongation [11]. Similarly, Zhao et al. also identified 36 meta-QTLs across 26 populations under stress and watered conditions using a meta-analysis, and several candidate genes were identified through fine mapping. Furthermore, a cluster of QTLs was detected on chromosome 3 and flanked by markers for plant height, TKW, and grain yield per plant, and these may be used to enhance maize drought tolerance by marker-assisted selection (MAS) in water-limited environments [35,37]. The clustered QTLs in maize also suggested that a cluster of genes, such as homeotic genes and other genes encoding transcription factors, regulates development, and that many plant responses to drought stresses rely on such genes' clustering.

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 [24]. 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. Similarly, Almeida et al. detected QTL in relation to GY with ASI and then introrse into a drought-prone maize line, showing increased grain and lower ASI [38]. Also, Bankole et al. 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 [39].

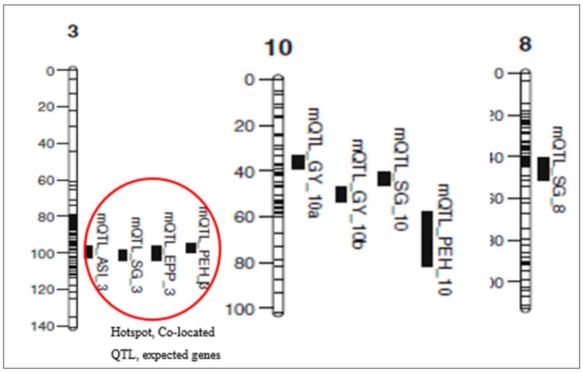

Figure 3: QTLs detected across chromosomes for ASI, ear per plant, stay green, plant height ear ratio under stress and water regime [33].

Genomic Wide Association Study (GWAS) for Drought Tolerance in Maize

Genome-wide association studies (GWAS) have been widely used to analyze the genetic control of complex traits for drought tolerance in maize. Wang et al. reported that 206 significant SNPs were associated with 115 candidate genes for drought tolerance and related to grain yield, its related traits, and secondary traits [40]. Moreover, 279 inbred lines were evaluated under field irrigated vs. stress conditions and insights into the genetic basis of drought tolerance at the flowering stage using GWAS and revealed that associated drought tolerance genes, candidate genes, and favorable alleles for variation provide insight into the genetic basis of drought tolerance at the flowering stage in maize

[41]. A Similarly diverse tropical maize line panel used to study the association of SNP with root traits and other physiological traits revealed that genes governing several functional traits [42-49].

Conclusion

Drought is one of the adverse environmental conditions that affect crop production, including maize. However, plants use different mechanisms to cope with the drought, such as escape strategies, drought avoidance, and osmatic adjustment. Taken into account in this situation, maize breeders, through conventional methods should consider secondary traits for selection under drought stress that are directly associated with grain yield. Several QTLs regulating important morpho-physiological traits were identified, molecular markers developed, and used to select donor parents with drought-adaptive alleles, which were 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.

Reference

1. FAOSTAT. Statistical data bases and data-sets of the food and agricultural orga nization of the United nations. 2021.
2. Thomson AMRA, Brown NJ, Roseberg R, Lazurade C, Benson V. Climate change impacts for the conterminous USA. An intergraded assessment, part 3. Dry land production of grains and forage crops. Climate change. 2005. 69: 43-65.
3. Cairns JE, Hellin J, Sonder K, Araus JL, MacRobert JF, et al. Adapting maize production to climate change in sub-Saharan Africa. Food Security. 2013. 5: 345-360.
4. Mulungu K, Ng'omb JN. Climate change impacts on sus tainable maize production in sub-Saharan Africa: A review. In A. Hossain (Ed.), Maize- Production and use. 2019.
5. Athar HR, Ashraf M. Photosynthesis under drought stress. Handbook of Photosynthesis (ed. M. Pessarakli), CRC Press, New York, USA. 2005. 793-804.
6. Nielsen RL. Assessing effects of drought on corn grain yield. West Lafayette, In: Purdue University. 2007.
7. Rhoads FM, Bennett JM. Corn. In: Stewart BA, Nielsen DR (eds) Irrigation of agricultural crops. ASA-CSSA-SSSA, Madison. 1990.
8. Edmeades GO. Progress in Achieving and Delivering Drought Tolerance in Maize: An Update. ISAAA, Ithaca. 2013.
9. Deikman J, Petracek M, Heard JE. Drought tolerance through biotechnology: improving translation from the laboratory to farmers' fields. Current Opinion in Biotechnology. 2011. 23: 1-8.
10. Paillard S, Schnurbush T, Winzeler M, Messmer M, Sourdille P, et al. An integrative genetic linkage map of winter wheat (Triticum aestivum L). Theoretical application Genetics. 2003. 170: 1235-1242.
11. Ribaut JM, Betran J, Monneveux P, Setter T. Drought Tolerance in Maize. In: Bennetzen J, Hake S, Eds. HandbookofMaize: ItsBiology, Springer, New York. 2009. 311-344.
12. Gowda VRP, Henry A, Yamauchi A, Shashidhar HE, Serraj R. Root biology and genetic improvement for drought avoidance in rice. Field Crops Research. 2011. 122: 1-13.
13. Rahul VD, Panda RK, Lenka D, Rout GR. Physiological and Biochemical Evaluation of Maize Hybrid Germplasm Lines for Drought Tolerance under Receding Soil Moisture Condition. Int J Curr Microbiol App Sci. 2018. 7: 2176-2191.
14. Maazou ARS, Tu JL, Qiu J, Liu ZZ. Breeding for Drought Tolerance in Maize (Zea mays L.). American Journal of Plant Sciences. 2016. 7: 1858-1870.
15. Banziger MG, Edmeades O, Beck D, Bellon M. Breeding for Drought and Nitrogen Stress Tolerance in Maize: from Theory to Practice. CIMMYT, Mexico, DF. 2000.
16. Lafitte HR, Blum A, Atlin, G. Using Secondary Traits to Help Identify Drought-Tolerant Genotypes. In: Fischer KS, Lafitte RH, Fukai S, Atlin G. Hardy B, Eds. Breeding Rice for Drought-Prone Environments, International Rice Research Institute, Manila. 2003. 37-48.
17. Banziger MG, Setimela PS, Hodson D, Vivek B. Agric Wat Manage. 2006. 80: 212-224.
18. Campos H, Cooper M, Edmeades GO, Loffer C, Schussler JR, Ibanez M. Changes in drought tolerance in maize associated with fifty years of breeding for yield in the US Corn Belt. Maydica. 2006. 51: 369-381.
19. Kumar M, Uniyal M, Kumar N, Kumar S, Gangwar R. Conventional and molecular breeding for development of drought tolerant maize cultivars. J. Crop Sci. Tech. 2015. 4: 1-3.
20. Zinselmeier C, Westgate ME, Schussler JR, Jones RJ. Low water potential disrupts carbohydrate metabolism in maize (Zea mais L) ovaries. Plant Physiol. 1995. 107: 385-391.
21. Lee EA, Tollenaar M. Physiological basis of successful breeding strategies for maize grain yield. Crop Science. 2007. 4: 202-2015.
22. Nepolean T, Hossain F, Shiriga K, Mittal S, Arora K, Rathore A. Unraveling the genetic architecture of subtropical maize (Zea mays L.) lines to assess their utility in breeding programs. BMC Genomics. 2013. 14: 877.
23. Menkir A, Dieng I, Gedil M, Mengesha W, Oyekunle M, et al. Approaches and progress in breeding drought-tolerant maize hybrids for tropical lowlands in west and central Africa. The Plant Genome. 2024. e20437.
24. Ribaut JM. Use of molecular markers in plant breeding: drought tolerance improvement in tropical maize. In Quantitative Genetics, Genomics, and Plant Breeding (Kang MS, ed.) CABI Publishing. 2002. 85-99.
25. Reynolds MP, Tuberosa R. Translational research impacting on crop productivity in drought-prone environments. Curr Opin Plant Biol. 2008. 11: 171-179.
26. Reynolds MP, Manes Y, Izanloo A, Langridge P. Phenotyping approaches for physiological breeding and gene discovery in wheat. Ann Appl Biol. 2009. 155: 309-320.
27. Chandel U. Morphological traits determining drought tolerance in local and cimmyt maize inbreds (Zea Mays L.). Agricultural Science Digest-A Research Journal. 2012. 32: 160-163.
28. Shadakshari TV, Shanthakumar G. Evaluation of maize inbred lines for drought tolerance under contrasting soil moisture regimes. Karnataka J. Agric. Sci. 2015. 28: 142-146.
29. Dordas CA, Papathanasiou F, Lithourgidis A, Petrevska JK, Papadopoulos I, et al. Evaluation of physiological characteristics as selection criteria for drought tolerance in maize inbred lines and their hybrids. Maydica. 2018. 63: 14.
30. Meseka S, Menkir A, Bossey B, Mengesha W. Performance Assessment of Drought Tolerant Maize Hybrids under Combined Drought and Heat Stress. Agronomy. 2018. 8: 274.

31. Ertiro BT, Beyene Y, Das B, Mugo S, Olsen M, Oikeh S, et al. Combining ability and testcross performance of drought-tolerant maize inbred lines under stress and non-stress environments in Kenya. Plant Breeding. 2017. 136: 197-205.
32. Chamarthi SK, Kumar A, Vuong T, Blair MW, Gaur PM, et al. Trait mapping and molecular Breeding in legumes: concepts and examples in soybean, common bean and chickpea. In: Pratap A, Kumar J (eds) Biology and breeding of food legumes. CABI International, Oxfordshire, UK. 2011.
33. Almeida GD, Nair S, Borém A, Cairns J, Trachsel S, et al. Molecular mapping across three populations reveals a QTL hotspot region on chromosome 3 for secondary traits associated with drought tolerance in tropical maize. Molecular breeding. 2014. 34: 701-715.
34. Li C, Sun B, Li Y, Liu C, Wu X, Zhang D, et al. Numerous genetic loci identified for drought tolerance in the maize nested association mapping populations. BMC genomics. 2016. 17: 894.
35. Zhao X, Peng Y, Zhang J, Fang P, Wu B. Identification of QTLs and Meta-QTLs for Seven Agronomic Traits in Multiple Maize Populations under Well-Watered and Water-Stressed Conditions. Crop Science. 2018. 58:507-520.
36. Yang XJ, Lu M, Zhang SH, Zhou F, Qu YY, et al. QTL mapping of plant height and ear position in maize (Zea mays L.). Yi Chuan= Hereditas. 2008. 30: 1477-1486.
37. Chen ZH, Cao ZY, Tang B, Li L. Mapping QTL for several drought related traits in maize (Zea mays L.) under field condition. Acta Agric Boreal Sin. 2012. 27: 79-86.
38. Almeida Gd, Makumbi C. Magorokosho S, Nair A. Borem JM, et al. QTL mapping in three tropical maize populations reveals a set of constitutive and adaptive genomic regions for drought tolerance. Theor. Appl. Genet. 2013. 126: 583-600.
39. Bankole F, Menkir A, Olaoye G, Crossa J, Hearne S, et al. Genetic gains in grain yield and other traits in a maize population improved using marker assisted recurrent selection. Frontiers in Plant Science. 2017. 8: 808.
40. Wang N, Wang ZP, Liang XL, Weng JF, Lv XL, Zhang DG, et al. Identification of loci contributing to maize drought tolerance in a genome-wide association study. Euphytica. 2016. 210: 165-179.
41. Zheng S, Chachar Y, Zhang Z, Zhou X, Zong G, et al. Dissection of Maize Drought Tolerance at the Flowering Stage Using Genome-Wide Association Studies. Genes. 2022. 13: 564.
42. Zaidi PH, Seetharam K, Krishna G, Krishnamurthy L, Gajanan S, et al. Genomic Regions Associated with Root Traits under Drought Stress in Tropical Maize (Zea mays L.). PLoS ONE. 2016. 11: e0164340.
43. Baret F, Madec S, Irfan K, Lopez J, Comar A, Hemmerle M, et al. Leaf-rolling in maize crops: from leaf scoring to canopy-level measurements for phenotyping. J Exp Bot. 2018. 69: 2705-2716.
44. Chen J, Xu W, Velten J, Xin Z, Stout J. Characterization of maize inbred lines for drought and heat tolerance. Journal of Soil and Water Conservation. 2012. 67: 354-364.
45. Landi P, Saungineti MC, Liu C, Li Y, Wang TY, et al. Root ABA1 QTL affects root lodging, grain yield and other agronomic traits in maize grown under well-watered and water stressed conditions. Journal of Experimental Botany. 2007. 58: 319-326.
46. Lunduka RW, Mateva KI, Magorokosho C, Manjeru P. Impact of adoption of drought-tolerant maize varieties on total maize production in south Eastern Zimbabwe. Climate and development. 2019. 11: 35-46.
47. Meuwissen TH, Hayes BJ, Goddard ME. Prediction of total genetic value using genome-wide dense marker maps. Genetics. 2001. 157: 1819-1829.
48. Monneveux P, Sánchez C, Beck D, Edmeades GO. Drought tolerance improvement in tropical maize source populations: evidence of progress. Crop Sci. 2006. 46. 180-19.
49. Nepolean T, Singh I, Hossain F, Pandey N, Gupta HS. Molecular characterization and assessment of genetic diversity of inbred lines showing variability for drought tolerance in maize. J. Plant Biochem. Biotechnol. 2013. 22: 71-79.