Kasetsart J. (Nat. Sci.) 44 : 507 - 516 (2010)

Review Article

Trends in Drought Research

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ABSTRACT

Drought is already a major abiotic constraint to global food production. Climate change will further aggravate this situation. Moreover, the expected increase in the world's population over the next decades will pose huge challenges to food production as the available water per capita decreases. Although several methods have been developed, it remains difficult to judge where water is and whether it will be scare.

Technological improvements will allow for more efficient irrigation. At the same time, it is vital to develop genetically improved crops, which produce higher yields under drought conditions. This can be achieved by increasing their yield potential and by reducing the gap between the maximum yield potential and yield under drought. For example, considerable progress has been made in the genetic improvement of temperate and tropical maize. Future progress will depend on newly defined secondary traits involved in the aerial morphology of plants, in the development and the architecture of the root system, and in physiological mechanisms that confer drought tolerance. There are many techniques available to achieve a better understanding of the complex network of plant responses to drought and to manipulate these responses. These techniques include the mapping of quantitative trait loci (QTLs), association mapping, studies of gene expression and genetic transformation. Although it is unlikely that single genes, especially genes protecting primary metabolism, will greatly enhance plant productivity in the field, some results are encouraging. The success of these technologies will depend on a multidisciplinary approach combining physiology, quantitative genetics, genomics and breeding. Moreover, the agronomical, socio-economical and political context must be considered in order to meet the tremendous challenges to crop improvement.

Keywords: drought, maize

INTRODUCTION

Water and society

Drought is a major abiotic constraint to agricultural production worldwide. The FAO considers drought to be the single most common cause of severe food shortage in developing countries, with more far-reaching consequences than other causes of food shortage, such as conflicts, flooding and economic mismanagement (Ribaut *et al.,* 2008). The situation will probably be aggravated further by climate change, resulting

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Received date : 02/06/09 Accepted date : 06/01/10

in more erratic weather, more frequent and stronger storms, with many regions of the world having higher temperatures and less precipitation (Sivakumar *et al.*, 2005). Although drought stress is also an issue in temperate regions, certain tropical regions will be affected to a greater extent.

However, the overriding global change that will occur during the next 40 years is a massive increase in the world's population (Wallace, 2000). This global change will pose enormous challenges to agriculture, particularly in Africa and Asia. The annual renewable water resources are largely fixed. Climate change may alter these resources to a certain extent, but compared to the changes in the availability of water per capita due to population growth, the impact of climate change on the renewable water resources is small (Wallace, 2000). Without significant improvements in the efficiency of water use in agriculture, the per capita availability of water for food production will decrease drastically.

It is difficult to estimate and even more difficult to predict the impact of decreases in the availability of water on global food security. Critical to these considerations is the question of whether water is scarce or whether it is used inefficiently (Rijsberman, 2006). First of all, it is important to determine how much water is required to produce enough food for today's population. Based on predictions of population growth and information about the renewable freshwater resources, it is possible to estimate the extent to which water is and will be scarce (Wallace, 2000).

Several indicators have been developed for this purpose (Gleick, 2002). The Falkenmark indicator or "water stress index" (Falkenmark *et al.*, 1989, 1997) is the most widely used. Based on the estimated demand of water for domestic use, for agriculture, for the environment, for industry and the energy sector, Falkenmark *et al.* (1997) proposed 1,700 m^3 of renewable water per capita per year as the threshold below which water stress occurs. Regions experience water scarcity when the water supply is below 1,000 m^3; below 500 m^3 the scarcity of water is extreme. The Falkenmark indicator is an intuitive measure and is easy to calculate. However, it does not take into account the infrastructure, which can change water availability. Variations in water requirements resulting from different lifestyles and climates are not represented either. Therefore, Ohlson (1999) proposed a modified Falkenmark indicator, which accounts for a society's capacity to adapt to water scarcity by technological, economic and other means.

The Water Resources Vulnerability Index (Shiklomanov, 1991; Raskin *et al.*, 1997) compares the annual withdrawal of water with the available water resources. Water withdrawal is defined as the amount of water removed from lakes, rivers and groundwater aquifers to satisfy human needs (Rijsberman, 2006). Water scarcity occurs in regions where 20 to 40% of the available water resources are used; when the withdrawal of water exceeds 40% of that available, water scarcity is severe. The Water Resources Vulnerability Index is more objective than the Falkenmark index but has limitations, too. The analysis does not take into account either how much water can be made available for human use through improved technology, or the proportion of withdrawn water that can be recycled. Moreover, there is no information about possible adaptation of the population to water stress.

The International Water Management Institute (IWMI) attempted to overcome these limitations by developing an indicator of physical and economic water scarcity. The IWMI analyzed the proportion of renewable water resources that is available to meet human needs; it differentiated between water consumption (e.g. evaporation) and water use, which allows for recycling (return of flow) and considered the adaptation through changes in the infrastructure and management (e.g. more efficient irrigation systems). Some countries will not meet the estimated demand for water in

2025 because water is physically scarce, whereas in other countries water is economically scarce. With considerable investments in infrastructure, these countries will be able to meet the estimated demand for water in 2025. Although the IWMI analysis is more precise than the Falkenmark indicator or the Water Resources Vulnerability Index, it still provides only a rough measure at a national scale.

According to the IWMI, 75% of the world's population lives in areas characterized by physical water scarcity. One billion people live in regions with economic scarcity (IWMI, 2006). Based on the United Nation's medium population projections of 1998, more than 2.8 billion people in 48 countries will face water stress or scarcity by 2025. Arid and semiarid regions account for approximately 30% of the total area of the world (Sivakumar *et al.*, 2005); 40 of the 48 countries in these regions are located in western Asia, North Africa or sub-Saharan Africa. By 2050, 54 countries could face water stress or scarcity, accounting for about 40% of the projected global population of 9.4 billion people (UNESCO, 2002).

Based on these predictions, there is an immediate need to increase water use efficiency and water productivity in agriculture. There is a large potential to increase water productivity by increasing the efficiency of irrigation systems. For example, it has been estimated that almost one third of irrigation water is lost in storage and conveyance (Bos, 1985). Surface runoff and drainage lead to further water loss; thus the efficiency of global irrigation systems is disturbingly low (approximately 37%) (Postel, 1993). Technological improvements, through, for example, the re-use of water, precision irrigation and precision agriculture, drip irrigation, partial root-zone irrigation or deficit irrigation based on measurements of the water status of individual plants or the whole canopy can largely increase irrigation efficiency (see Parry *et al.*, 2005, for a short overview).

Maize yield under drought

The water productivity of crops must also be increased. This is particularly important in rainfed agriculture. The resulting benefit is two-fold: On the one hand, food security in rainfed systems will be better and on the other, the overall water balance will be more favorable. The more food produced in rainfed systems, the smaller the demand for freshwater resources for irrigation (Wallace, 2000). Genetic improvements (i.e. more drought-tolerant crop varieties) cannot counteract all drought-induced yield losses but, nevertheless, will contribute considerably to global food security. Poor farmers in particular can readily benefit from genetic improvements, which are incorporated in the seed and do not depend on agronomic techniques, on experience in soil and crop management, on the availability of inputs, on infrastructure or access to markets.

Passioura (2006) distinguished three factors involved in improving yield under water-limited conditions, by developing and growing plants that 1) transpire more water, 2) exchange the transpired water more efficiently for CO_2 in order to produce more biomass, and 3) allocate more biomass to the grains (or to the harvestable part). Considering the plant only, these components can be addressed by altering the morphology and the physiology of the crop. The crop's response to stress depends on numerous traits, many of which are constitutive, but which may also be modified by stress. According to the definition of drought tolerance by Cooper *et al.* (2006), a drought-tolerant genotype produces higher yields than a drought-susceptible genotype in a variety of water-stressed environments. The ideal genotype combines both a high yield under favorable conditions with tolerance to water stress. The overall goal of breeding for drought tolerance is, therefore, to realize a high maximum yield potential and to reduce the gap between yield potential and yield under stress. Research in plant science must identify drought-tolerance traits and manipulate these traits by "conventional" breeding, marker-assisted breeding or gene transformation, as demonstrated here for maize.

Duvick (2005) gave a comprehensive overview of the contribution of breeding to the improvement of yield in temperate maize. About 50% of the on-farm increase in the yield of hybrid maize during the last 60 to 70 years has been achieved through genetic improvements, mainly by the better tolerance to stress that has been incorporated into newer hybrids. The increase in yield was accompanied by changes in a number of morphological and physiological traits, for example plant height, the anthesis-to-silking interval (ASI), staygreen, logging resistance and more efficient photosynthesis, as well as an improved photosynthetic rate after stress events (Duvick, 2005). These advances were achieved mainly by selection in rainfed nurseries, which are seldom prone to drought and in which the plants were grown at high planting densities. This measure is especially efficient in maize breeding: maize has evolved from a single-plant ecosystem, whereas small-grain cereals have undergone continuous and considerable intra- and inter-specific competition. Therefore, selection at high planting densities improves the tolerance of maize to intraspecific competition and suboptimal light conditions in the canopy. Large populations were grown under these conditions and inbred lines with stable yields were recycled (Bruce *et al.*, 2002).

Considerable progress in the genetics of tropical maize was also achieved, leading to a higher yield potential and improved drought tolerance (Heisey and Edmeades, 1999; Bänziger *et al.*, 2000; Monneveux *et al.*, 2006b). Breeding for drought tolerance at flowering, the developmental stage, at which maize is most susceptible to drought (Claassen and Shaw, 1970; Westgate and Boyer, 1985), has identified key secondary traits for grain yield, with the anthesis-to-silking interval being the most prominent one. The ASI was very useful in identifying genotypes with a high level of stress tolerance; there was considerable genetic variability in ASI, the ASI was negatively associated with grain yield, it was a good predictor of hybrid performance, and it was easy and cheap to record (Edmeades, 1997). However, as a consequence of continuous selection for a short ASI, the association between grain yield (grain abortion) and ASI decreased over time (Monneveux *et al.*, 2006a). Once the ASI of elite germplasm is sufficiently short, a further reduction is unlikely to generate significant genetic gains (Byrne *et al.*, 1995). Hence, it is necessary to identify novel secondary traits in order to predict the performance of maize genotypes under drought. Further progress in drought tolerance will probably depend on changes in the areal architecture, which has a strong impact on the partitioning of assimilates and the radiation use efficiency (Ribaut *et al.*, 2008); however the architecture of the root system and physiological mechanisms that confer drought tolerance will play a significant role also.

Based on the progress in improving drought tolerance of tropical maize, the ideotype of a drought-tolerant maize plant is characterized by short plants, reduced leaf area (especially on the upper part of the stem), small tassels, thick stems, erect leaves, delayed senescence, deeper rooting (with less lateral branching), better grain filling capacity, robust growth of spikelets and kernels and good osmotic adjustment at low water potential (Ribaut *et al.*, 2008).

Examples of drought research by ETH Zurich, Institute of Plant Sciences

The importance of these traits can be illustrated for two tropical maize inbred lines that were used to develop a segregating mapping population of recombinant inbred lines (RILs) at the International Maize and Wheat Improvement Center (CIMMYT) in Mexico. CML444 was developed at CIMMYT in the 1990s. It has a compact phenotype with strong, erectophilic, darkgreen leaves and produces high yields under drought, despite a relatively low drought-tolerance index (DTI; defined as the yield under severe stress divided by the yield under non-stress conditions) as a result of its high yield potential under optimal growing conditions. SC-Malawi was developed in Zimbabwe in the 1960s and has long, horizontal, light-green leaves, short internodes at higher positions on the stem, a relatively low yield under stress but, due to its low yield potential, it has a high DTI. Several field experiments conducted at CIMMYT in Mexico and Zimbabwe with drought stress at flowering and under well-watered conditions showed that CML444 performed better than SC-Malawi because of better constitutive traits conferring high plant vigor across water regimes (Messmer *et al*., 2009).

Experiments conducted at the Swiss Federal Institute of Technology (ETH), Zurich, showed that young CML444 plants (up to the 5-leaf stage) produce a deeper root system than that of SC-Malawi and extract more water from deeper soil layers. At the 8-leaf stage, CML444 also produces longer axile roots, essential for a greater vertical (and horizontal) distribution of the root system than SC-Malawi (Hund *et al*., 2009). Similar differences between these lines were also detected at the 2-leaf stage in a high-throughput phenotyping platform for root traits (Trachsel *et al*., 2009). These apparently constitutive differences in the architecture of the root system may also be expressed in the field and may be associated with the good drought tolerance of CML444. However, the relationship between root traits and drought tolerance of maize is still unclear. Recurrent selection in tropical maize populations has reduced root biomass and inbred lines with poor early root development had higher yields under drought than inbred lines with vigorous early development of roots (Bruce *et al*., 2002). However, the root system of the latter could have reached deeper soil layers (Hund *et al*., 2008).

Further root studies were done by Ruta *et al*. (2010) at the 2-leaf stage in the high-throughput phenotyping platform for root traits (see above) with RILs of another CIMMYT mapping population, derived from the cross between Ac7643 (P1) and Ac77290/TZSRW (P2). P1 has a short ASI and a relatively high yield under drought, in contrast to P2 (Ribaut *et al*., 1996). Quantitative trait loci (QTLs) for the shoot-to-root weight ratio and leaf area-to-root length ratio collocated with QTLs for ear number under water stress; this could be an intriguing indicator that the well-known adaptive mechanism, favoring root development over shoot development after the onset of drought, enables the plant to produce a more stable yield under drought in the field. An increase in the growth of axile roots seemed to be linked to a decrease in ASI; the alleles of the drought-tolerant parent, P1, increased the number of crown and seminal roots, while the alleles of P2 increased the ASI at both loci. This is an important indication that the genes responsible for early proliferation and elongation of axile roots may be active at later growth stages, too. These QTLs collocated with QTLs for root pulling force from another marker population (Sanguinetti *et al*., 1999; Tuberosa *et al*., 2002b); thus it is expected that there is a relationship between the number of axile roots of seedlings and a well-structured architecture of the root system at later stages.

Marker-assisted breeding

The advent of molecular markers opened up the possibility of identifying genomic segments involved in the genetic control of target traits under stress and non-stress conditions. Drought tolerance is a complex and multigenic trait, although single genes, controlling, for example, the time of flowering or osmotic adjustment (OA), may also be involved in the plant response to drought. A large amount of QTL data from segregating populations has been gathered over the last two decades. The genetic control of target traits differed between plants under drought-stressed and well-watered conditions. Therefore, breeding for drought tolerance will be efficient when conducted under stress (Messmer *et al.*, submitted). QTLs identified under stress tend to cluster in genomic regions related to drought tolerance, whereas those identified under well-watered conditions are related to plant performance. Nevertheless, clusters of QTLs are also found in both water regimes and are probably involved in the broad adaptation of plants (Ribaut *et al.*, 2008). However, Tuberosa *et al.* (2002a) compiled a single genetic map of QTLs from various studies and found that drought-related QTLs were dispersed throughout the maize genome. As QTLs are specific to their original genetic background and the effect of single genes on target traits is usually weak, the number of successful marker-assisted breeding (MAB) experiments for improved drought tolerance is limited.

This draws attention to the development of new MAB strategies, which go beyond marker-assisted back-crossing or marker-assisted recurrent selection. MAB strategies based on genomic regions involved in the drought response across germplasm and environments, as identified through meta-analyses, would enable the use of the large amount of genomic data and would circumvent the need to identify QTLs in each target cross. The possibility of linkage drag and the lack of contrasting alleles may limit such approaches (Ribaut *et al.*, 2008). A logical extension would lead to “breeding by design” (Peleman and van der Voort, 2003) with the objective of stacking the favorable alleles from several parental lines at each of a large number of loci under selection.

Most of the information on drought tolerance is based on single genotypes and experimental mapping populations. Association studies, however, are more powerful in identifying useful allelic variation than QTL mapping, because the former explore the results of many generations of recombination and selection (Syvänen, 2005). Informative markers, resulting from association mapping, are usually functional in diverse genetic material and are suitable for MAB. In maize, however, the low level of linkage disequilibrium compared to other species, poses methodological and technological challenges for association mapping.

Combining QTL mapping and association mapping has great potential for maize breeding. The overall goal of both approaches should be to investigate the effect of quantitative traits on yield across different levels of water supply in order to identify and combine alleles that increase crop productivity. As stated by Ribaut *et al.* (2008), a key consideration should be the need to explore alternative segregating populations and approaches to selection, which can take advantage of the increasing ability to define the alleles that are the most desirable at multiple target loci, rather than focusing only on the role of markers in conventional breeding.

Advanced molecular pathways to drought tolerance

With the genomic tools available, it is now possible to study the expression of thousands of genes. Many drought-responsive genes have been identified and manipulated during the last decade, including the examples of genes involved in the biosynthesis of osmolytes, genes related to scavenging active oxygen, or genes encoding molecular chaperons, signaling molecules, and transporters or transcription factors (see Araus *et al.*, 2003; Wang *et al.*, 2003; Parry *et al.*, 2005). Transcription factors may be suitable for the genetic engineering of complex traits, unless they activate additional genes that have a negative effect on crop performance. Stress-inducible promoters could circumvent this limitation by avoiding negative effects on crop performance under non-stress conditions and, at the same time, allow for improved drought tolerance under stress conditions. However, most of the drought-responsive genes identified thus far are related to primary metabolism and protect and maintain the structure and function of cells at low water potential (Parry *et al.*, 2005). Protection of the primary metabolism is required only when plant tissues are dehydrated under severe drought stress. Hence, genes protecting the primary metabolism mainly contribute to plant survival rather than to productivity and may even have a negative effect on productivity. Moreover, most of the genetic transformations were done with model species and/or in the laboratory. Only a few of these transformations have been validated in first-phase trials under field conditions (Dunwell, 2000). Nevertheless, there are examples of successful genetically engineered crops (for a short review, see Cattivelli *et al.*, 2008): transgenic wheat, expressing the *DREB1A* transcription factor (Pellegrineschi *et al.*, 2004), rice plants, over-expressing the *SNAC1* transcription factor (Hu *et al.*, 2006), and rice plants with ectopic expression of *OsCDPK7*, a calcium-dependent protein kinase (Saijo *et al.*, 2000).

Transpiration efficiency depends mainly on the photosynthetic pathway. C_4 plants, such as maize and sorghum, produce about twice to three times as much biomass per unit of transpired water as C_3 plants, mainly because they concentrate CO_2 at the carboxylation sites. Moreover, their optimum temperature for growth is higher; hence C_4 plants produce higher yields in warm climates. Increasing mesophyll conductance for CO_2, as a means of improving photosynthesis at a given stomatal conductance, is not yet possible, but may become possible, because aquaporins seem to play a role in CO_2 conductance (Uehlein *et al.*, 2003; Hanba *et al.*, 2004; Parry *et al.*, 2005). Introducing a form of Rubisco with higher specificity to CO_2 could increase the photosynthetic efficiency of C_3 crops. Recent work on Arabidopsis showed that this might be possible in the future: The *ERECTA* gene resulted in higher water-use efficiency, irrespective of water availability (Masle *et al.*, 2005). Genes that simultaneously increase water-use efficiency and photosynthesis have great potential for improving the drought tolerance of crops, but their usefulness under realistic field conditions has yet to be proven. Thus far, improving water-use efficiency, a key component of improving the water productivity of crops, is usually accompanied by a lower rate of photosynthesis and lower yield (Parry *et al.*, 2005).

Finally, at the 50th Annual Maize Genetics Conference in Washington D.C. in 2008, Monsanto presented a "proof of concept" from the private domain, illustrating the enhancement of drought tolerance of maize by genetic transformation. Monsanto scientists permanently activated a maize gene equivalent to the *Arabidopsis NF-YB1* gene. Transformed maize plants produced yields that were about 10 to 15% higher under a variety of stress conditions, but the yield increase did not exceed that of natural variation.

CONCLUSION

Progress in maize breeding during the last century has shown that improved genetics contributed to about 50% of the advances in improving yield. Today, marker-assisted breeding is becoming the standard breeding approach. An increasing body of information on the genetic control of target traits and on physiological mechanisms conferring drought tolerance is available. Biotechnology has opened-up new possibilities for creating and managing genetic variation, which is the key to crop improvement. These technologies will evolve rapidly and can greatly facilitate further progress in research into drought. Moreover, these technologies will also become available for crops of regional importance. The merits of biotechnology should, however, not be exaggerated. A multidisciplinary approach, combining quantitative genetics, genomics, physiology and breeding is probably the best route for improving the drought tolerance of crops, for enhancing water productivity, and, thus, for ensuring food security. Phenotyping in the field under carefully managed stress conditions will be of crucial importance, because the differences between genotypes may be small and because essential traits after the ASI may not allow for high-throughput phenotyping. The success of today's breeding programs can be determined from yields at maximized inputs. For example, maize yields in the Ivory Coast increased from 1.5 t ha^{-1} for open-pollinated varieties to 10 t ha^{-1} for Thai hybrids, as found in recent Syngenta Sochim trials. Future progress will greatly depend on improved genetics. However, the agronomical context, as well as socio-economic factors and policy, must be taken into account; they influence to a large extent whether farmers adopt improved varieties and whether they can minimize the gap between yield potential and on-farm yield.

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