Progress in Achieving and Delivering Drought Tolerance in Maize - An Update

by

Greg O. Edmeades

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Preface: Special Feature on Drought Tolerance in Maize

The proverb ***"Water is the staff of life"*** reminds us that water is important and precious. Agriculture currently uses over 70% (86% in developing countries) of the fresh water in the world. Water tables are dropping fast in countries like China, and water supplies will continue to shrink worldwide as global population will grow from the current 7 billion to more than 9 billion people in 2050. Whereas people drink only 1 to 2 liters a day, the food and meat we eat in a typical day requires 2,000 to 3,000 liters to produce. Both conventional and biotechnology approaches are instruments to develop crops that use water more efficiently and are more tolerant to drought. Given the lack of water and its cardinal role in crop production, it follows that tolerance to drought and efficient water usage should be assigned the highest priority in developing future crops. The situation will be further exacerbated as global warming takes its toll, with weather expected to become generally drier and warmer, and as competition for water intensifies between people and crops.

Drought tolerance conferred through biotech crops is viewed as the most important trait that will be commercialized in the second decade of commercialization, 2006 to 2015, and beyond, because it is by far the single most important constraint to increased productivity for crops worldwide. Drought tolerant biotech/transgenic maize, is the most advanced, and the first biotech maize will be launched commercially in the USA in 2013. Notably, a private/public sector partnership (WEMA) hopes to release the first biotech drought tolerant maize as early as 2017 in sub-Saharan Africa where the need for drought tolerance is greatest.

Given the pivotal importance of drought tolerance, ISAAA invited Dr. Greg O. Edmeades, former leader of the maize drought program at the International Maize and Wheat Improvement Center (CIMMYT), to contribute a timely global overview on the status of drought tolerance in maize, in both conventional and biotech approaches, in the private and public sector, and to discuss future prospects in the near, mid and long term. The contribution by Dr. Edmeades, ***"Progress in Achieving and Delivering Drought Tolerance in Maize - An Update"***, supported by key references, was originally published in ISAAA Brief 44 as a special feature to highlight the enormous global importance of the drought tolerance trait, which virtually no crop or farmer in the world can afford to be without. Of all the water on earth, only 0.003% is available for human consumption hence using water at current rates when the world will have to support 9 billion people or more in 2050, is simply not sustainable. The review on drought tolerant maize is particularly relevant to sub-Saharan Africa, because of the urgent humanitarian need to boost the yields of maize, which is the staple food for more than 300 million people, a significant proportion of whom are suffering from hunger and malnutrition.

Dr. Clive James
Chairman, ISAAA Board of Directors

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Abstract

Drought in 2012 through much of US Midwest has led to reductions of 15% and 21% in national maize production and maize yields, respectively, and cast a sharp focus on progress towards drought tolerance in this important crop. Drought also continues to destabilize maize yield in major regions of sub-Saharan Africa where irrigation is not feasible, with a direct human cost. Maize yield under drought mainly reflects tolerance to water stress of the kernel setting mechanism at flowering.

Genetic improvement can probably close 20-25% of the yield gaps between drought-affected and optimal conditions. Conventional selection by CIMMYT specifically for drought tolerance focused on yield and associated secondary traits has resulted in gains of around 100 kg/ha/yr, in tropical maize populations. Selection by the private sector in temperate germplasm, based on multi-location trials for general performance has given gains under drought of ~65 kg/ha/yr. Heat tolerance is becoming more important as climate changes, and the genetic controls of heat and drought tolerance are largely independent of each other. Representative managed stress environments have been endorsed as an important component of efficient selection for drought or heat tolerance. Marker-assisted selection (MAS) is now having a significant impact, and when well executed could double gains from conventional drought tolerance selection. Current seed company claims, based on 2012 US data, appear to show Syngenta's Agrisure Artesian™ and Pioneer's AQUAmax™ hybrid products, selected using native genes and MAS, out yielding competing hybrids by around 500 kg/ha, while Monsanto's Droughtgard™ transgenic hybrids out yielded AQUAmax hybrids by a further 300 kg/ha. The Droughtgard event, MON87460 will be available to farmers royalty-free under the WEMA Project in five countries in sub-Saharan Africa, hopefully from 2015 onwards. Product delivery of drought tolerant hybrids remains a challenge in sub-Saharan Africa, but private seed sector capacity is increasing rapidly. Large publicly funded projects are now supplying drought tolerant inbreds and hybrids to national and regional seed companies in sub-Saharan Africa and South Asia. Public-private partnerships, though still rare, are using cutting edge doubled haploid, MAS and transgenic technologies to develop drought tolerant hybrids and deliver them successfully to smallholders in sub-Saharan Africa.

Experience since 2008 has reduced expected gains under drought in a commercial maize breeding context, with the exception of MAS.

Starting with a base yield of 3 t/ha under drought, conventional breeding for regional adaptation should reliably deliver 50 kg/ha/yr (~1.4%/yr). MAS, which has performed well in the recent past, can boost these by a further 25 kg/ha/yr (~0.6%/yr) with potential for significantly larger gains from newer methodologies. The slower than expected development of transgenic drought tolerance suggests gains of 30 kg/ha/yr (0.7%/yr), assuming one new transgene is available every eight year that lifts yield 5% per transgene. Over the next two decades gains of 1.4, 2.0 and 2.7% per year can be expected from conventional selection, conventional + MAS, and conventional + MAS + transgenes, respectively. Greater gains are probable if genomic selection attains its potential and drought transgenes can be efficiently stacked. Impacts could be realized much sooner if harmonized biosafety and hybrid release policies was adopted. Germplasm collections are assuming greater importance if gains from native genes are to be sustained. Efficient and accurate field phenotyping remains essential for genetic progress. In sub-Saharan Africa trained and well-supported field staffs are urgently needed. Emerging private-public partnerships in crop development and a strong private seed sector will be more than adequate to meet these challenges as long as our resolve does not falter and we use our resources efficiently.

Introduction

Drought has major implications for global food supply because of the expected effects of gradual climate change over the next century, and the variation in climatic extremes in the short term that it is expected to bring. Although increased temperature is a more predictable outcome than changes in rainfall patterns accompanying climate change, it is generally considered that major maize producing areas will become warmer, drier and subject to an evolving array of maize diseases and pests that are new to those areas.

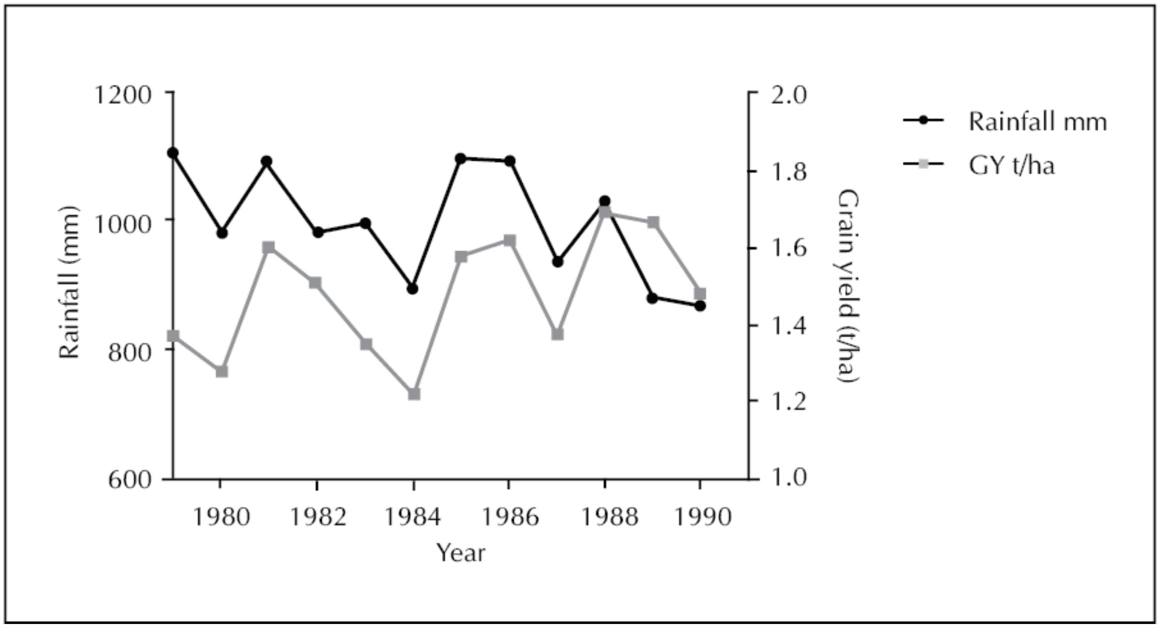
These trends were apparent four years ago when an earlier review of progress in drought tolerance in maize was published (Edmeades, 2008), but their relevance has been brought sharply into focus by the severe drought encountered in the central and south of the US Corn Belt during 2012, with effects being felt as far north as Canada. The United States normally produces 38% of the world's maize (FAOSTAT, 2012), so the reductions of 21% and 15% in US maize yields and production in 2012, compared with 2009-11 mean levels, has implications globally (http://quickstats.nass.usda.gov/). The EU-27 countries produce around 12% of global maize, and their yields in 2012 have also been reduced by an average of 12.5% by heat and drought (MARS, 2012). With this in mind, it was decided to review again the status of drought tolerant maize germplasm and its supply. This review will follow the same general outline of Edmeades (2008), summarizing the key points from that review and updating with new information as appropriate.

1. Drought and maize: the scope of the problem

Maize is the cereal with the largest annual global production at 829 M tons annually (vs. 690 M t/yr for rice and 675 M t/yr for wheat). Maize grain yields in the temperate developed world of North America and Europe average 8.7 ton/ha vs. 3.7 t/ha in less developed tropical countries of Asia and Africa (FAOSTAT, 2012). In both production environments drought is the most important abiotic stress constraining and destabilizing maize grain production. Its effects are particularly severe in southern and eastern Africa where most maize is rainfed. For example, in the period 1990-2009 mean yield of South Africa had a coefficient of variation (CV) of 23% vs. 7% for the US on mean yields of 4.1 and 9.8 t/ha (FAOSTAT, 2012).

Most of the 160 m ha of maize grown globally is rainfed. The proportion of the crop area irrigated in the US is around 14%, in China 40% and in Egypt close to 100%, but in most other countries it is often less than 10%. Losses of yield to drought annually are thought to average around 15% of well-watered yield potential on a global basis, a figure that equates to 120 M tons of grain. At today's prices this is worth around $36 billion, but the real costs are in terms of human welfare in sub-Saharan Africa where maize is a staple food for more than 300 million people. Drought often afflicts whole regions, such as eastern and southern Africa (Figure 1), or the Sahel and the Sudan savannas of West Africa in 2011, creating regional food shortages that cannot easily be alleviated by cross-border trade. The production of maize in southern Africa fluctuated from 12.5 million tons in 1992 (a drought year) to 23.5 m tons in 1993 (Bänziger and Araus, 2007). In 2011, a year of moderate food relief activity, the World Food Program purchased 410,000 tons of maize worth more than $100 M today for sub-Saharan Africa (WFP, 2012). Drought-tolerant maize could still play a significant part in meeting the Millennium Development Goal of "halving by 2015 the share of people suffering from extreme poverty and hunger."

Figure 1. Maize grain yield in selected East and Southern African countries is directly affected by rainfall recorded in maize growing areas during the season (unpublished data, CIMMYT).



Regional and national yields only tell part of the story. In fields with varying topography, texture and thickness of topsoil, yields may vary ten-fold. The normal practice of sowing a single variety or hybrid in such a field implies the need for a good level of drought tolerance to reduce this level of within-field yield variation.

The prospects of adding additional irrigated land on which maize will be grown are relatively slight, given that irrigated land area is projected to increase at a rate roughly equal to or less than the population growth rate. As well, there is a steady decline in many of the water tables in key food producing areas such as the North China Plain, the Indo-Gangetic Plain and in the High Plain states fed by the Ogallala aquifer in the US. A recent study suggests that the greatest water shortages will be encountered in the basins of the Niger, Ganges and Yellow Rivers that feed 11.6% of global population, and India's food supply is at risk because it uses 25% of all water used in agriculture globally (Knight et al. 2012).

Trends due to climate change and reduced soil quality all suggest an increased need for drought tolerance – but increasingly linked to heat tolerance as well. A recent study by Lobell et al. (2011) noted that about 65% of the maize growing areas of Africa would experience yield losses if there was a 1°C increase in mean temperatures under well-watered conditions. They estimated that this would rise to 100% of any area that was under drought. Improvements in drought and heat tolerance would presumably offset this trend. A 1°C rise in average temperature is also estimated to increase the intensity of the global water cycle by 8% due to increased evaporation rates (Knight et al. 2012).

The yield gap between well-watered crop potential yield and water-limited yield is often large, but as a rough rule of thumb 20-25% of this gap could be eliminated by genetic improvement in drought tolerance and a further 20-25% by application of water-conserving agronomic practices. The remaining 50-60% can only be met by irrigation – when available and affordable (Edmeades et al. 2006). This review focuses on the genetic improvement of drought tolerance and to a lesser extent heat tolerance. However, equally important will be the improvement and use of water saving agronomy such as drip irrigation and conservation tillage, as well as reductions in losses through leaks in major irrigation structures.

2. How maize responds to drought and heat stress

Typical visual symptoms of drought stress in maize are a change in color from green to green-gray, and rolling of the lower leaves followed by those in the upper canopy. At the same time stomates are closing, photosynthesis is being sharply reduced and growth is slowing. When stress coincides with the 7-10 day period prior to flowering, ear growth will slow more than tassel growth and there is a delay in silk emergence relative to pollen shed, giving rise to an interval between anther extrusion and silk exposure. This anthesis-silking interval (ASI) can be used to predict drought-induced yield reduction. At the same time leaf senescence begins at the base of the plant and spreads upwards to the ear. Severe stress at flowering may lead to the complete abortion of ears and the plant becomes barren. Drought-affected ears typically have fewer kernels that will be poorly filled if drought extends throughout grain filling (Edmeades et al. 2000).

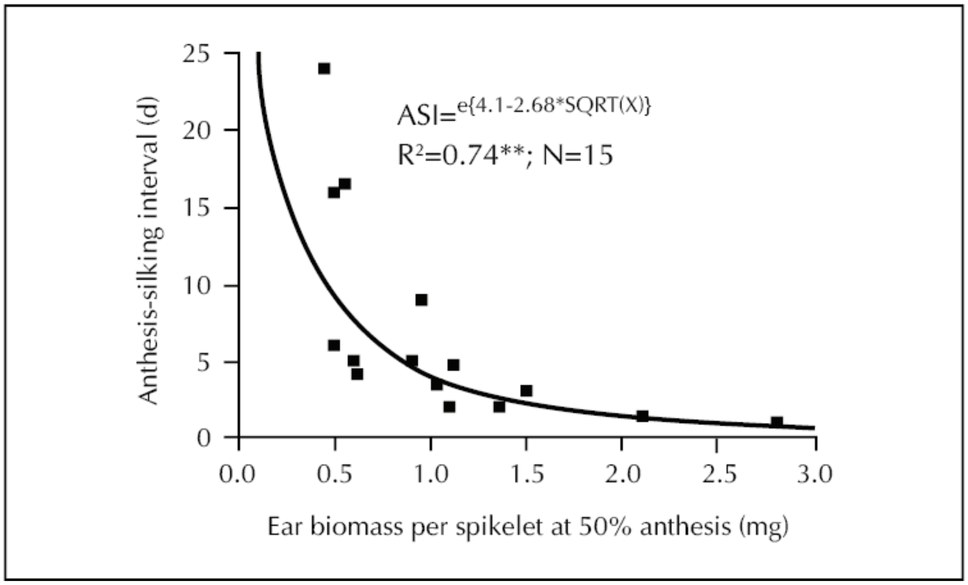
Genetic and management strategies that target improved grain yields in a water-limited environment target three variables (Passioura, 1977). These are the amount of water captured by the plant (W), the efficiency with which that water is converted to biomass (water use efficiency, WUE), and the harvest index (HI) or the proportion of biomass forming grain. Each of these variables can be altered. Osmotic adjustment of roots of temperate maize can increase the amount of water taken up from a drying soil (Chimenti et al. 2006), but increasing root depth through genetic control of morphology is likely to be a more effective means of increasing W. Development of a deeper rooting habit is effective when there are no physical barriers to root growth, and the wetting front from rain or irrigation extends downwards beyond the rooting zone. Research suggests that deeper roots are needed rather than an increase in root biomass, and variation for root depth occurs among genotypes (Edmeades et al. 2006). Apart from the obvious step of irrigation, other growing practices can alter W substantially. Good weed control and the managed variation in plant density are practices that control the amount of water available for transpiration.

WUE is maximized by early planting of crops, and by maintaining healthy leaves with high levels of nutrients (Passioura and Angus, 2010). Extending “stay green” through selection for delayed leaf senescence is generally considered important for maintaining WUE and root health, and also for increasing the duration of kernel filling -- though the relationship between stay green scores and grain yield under drought is often weak (Chapman and Edmeades, 1999). Blum (2009) noted that selecting only for WUE however may reduce yields and argues that effective use of water (EUW) implying maximum water capture and conversion to grain should be the goal. From a practical breeding perspective the two approaches (WUE and HI vs. EUW) are similar.

The numbers of kernels set and filled under drought stress accounts for most of the variation in maize grain yield under drought (e.g., Bolaños and Edmeades, 1996; Edmeades et al. 2000; Barker et al. 2005), and directly affects HI. Kernel number is largely determined at flowering. The slower growth of ears under drought sometimes means that pollen is shed before silks emerge, and in very uniform hybrids with small tassels pollination may fail because of pollen shortage. Generally however, the slow growth of the ear prior to silking is reflected in slow growth and small size of ovules, weak silk growth and a failure to set grain even when pollinated with adequate amounts of fresh pollen. In extreme cases no silks may emerge from the husk, and the plant becomes barren.

Events at flowering play a critically important part in yield stability (or lack of it) under drought. Partitioning of assimilate to the developing ear directly affects ovule growth at flowering and the ASI (Figure 2). Modern crop improvement has increased assimilate flow to the developing ear so kernel set is stabilized and grain yield is increased, and ASI is one trait that is extensively used for this purpose. In highly selected temperate maize, improvement in yield has been attributed largely to increases in stress tolerance, in part through this mechanism (Duvick et al. 2004; Tollenaar and Lee, 2011). However, there is also evidence that ASI has been improved in modern hybrids to a level where its correlation with grain yield is declining, and that selection for traits such as synchronous silk emergence on the ear may drive further increases in kernel set under drought (Schussler et al. 2011; Araus et al. 2012).

Figure 2. Relationship between ear biomass per plant at 50% anthesis and the anthesis silking interval observed in the same plots (modified from Edmeades et al., 1993).



Kernel set must be followed by kernel filling to ensure that yield potential is realized. Kernels near the tip of the ear will often abort after several weeks of growth if drought-affected. Remobilized assimilate stored in the stem prior to and during the flowering period normally plays a role in buffering filling rate only in the last half of filling. Maintaining an active green leaf area plays a role in reducing effects of drought during grain filling on kernel final weight. A component of this is resistance to photo-oxidation of chlorophyll (or bleaching when there is an imbalance of excitation pressure – see Hüner et al. 2012) by bright sunshine striking a leaf that has lost its turgor and its capacity to photosynthesize at normal rates.

Heat tolerance is becoming increasingly important. High temperatures are often, but not always, associated with drought since transpiration which cools the crop is sharply reduced as leaves begin to roll. The effects of temperature on growth and development are well known – warmer temperatures increase development rate more than photosynthetic rate, so less assimilates is available per growth stage, resulting in reduced yields. Yields decline, but crops will mature more rapidly. Replacing existing hybrids with selections that are later maturing will partially offset this trend.

A more serious issue arises when high temperature spikes coincide with the susceptible growth stages in maize of flowering and early grain fill, and farmers can do little to alleviate this stress. Adaptation to heat stress is defined by Cairns et al. (2012) as tolerance to “temperatures above a threshold level that results in irreversible damage to crop growth and development." They note that this threshold is lower for reproductive organs than for vegetative structures. Pollen viability in Corn Belt germplasm was reduced when severed tassels were held at 38°C (Schoper et al. 1987), but the degree of damage varied by hybrid. Female tissues are thought to be more tolerant to heat in maize. However, Edreira et al. (2011) reported increased pollination failure and a large increase in kernel abortion when ears were heated and held at 33-40°C. High temperatures also reduce leaf area and accelerate leaf senescence (Cairns et al. 2012) but there are clear and heritable differences among inbred lines in tolerance to temperatures exceeding 40°C in the field (Chen et al. 2012). Root elongation in maize seedlings is also reduced by high temperatures (Trachsel et al. 2010), though differences in the temperature response of the rate of elongation of roots and leaves are much greater among species than within (Parent and Tardieu, 2012). There is increasing evidence that tolerances to drought and heat are under independent genetic control, and can be treated as two distinct traits (Cairns, pers. comm., 2012).

Our understanding of key genetic controls of root morphology, functional stay green, and of key processes affected by high temperatures is relatively incomplete. It is generally agreed that drought tolerance from a breeding viewpoint is a complex trait that shows a high level of genotype x environment (G x E) interaction (Cooper at el. 2006) – though from the physiological viewpoint it can be simplified into several clear processes (Blum, 2011). Heat tolerance appears to be less complex, but there is little published evidence to date confirming this assertion.

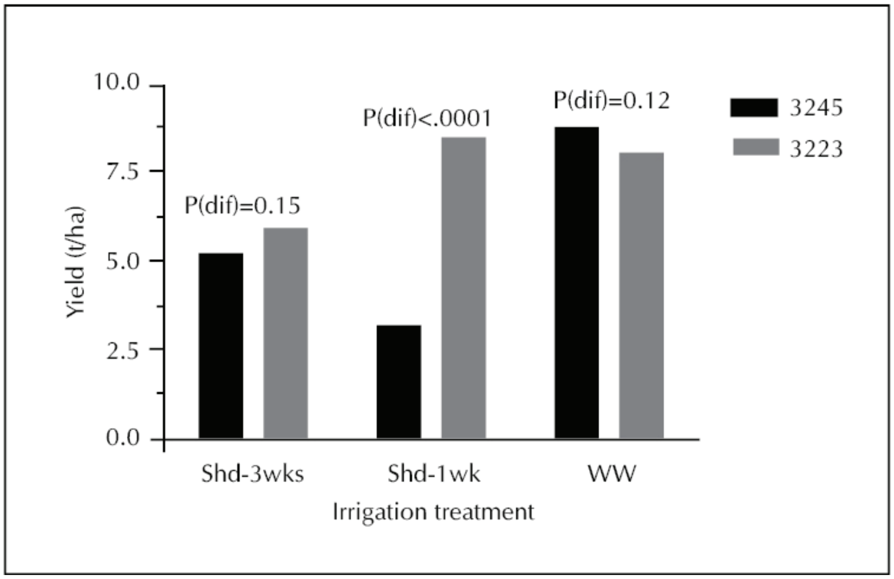
3. Development of drought tolerant hybrids

a. Requirements for successful development of drought-tolerant products

Identifiable and heritable genetic variation for tolerance to drought or heat within a breeding population is first basic requirement for genetic progress in stress tolerance. Abraham Blum, a stress breeder of immense experience, suggested that stress tolerant alleles are present at low frequencies in most elite breeding populations, so these populations should be evaluated first (Blum, 1988). Evidence for useful genetic variation in elite breeding pools is found in significant levels of G x stress level interaction in response to drought stress (Figure 3). Arnel Hallauer, another widely respected breeder, frequently noted that the most important choice for a breeder was the breeding population chosen for improvement (Hallauer and Miranda, 1988). Unimproved sources such as landraces, while sometimes possessing unique alleles, are low yielding and are often poorly adapted and therefore difficult to evaluate.

What traits are important? The most useful genetic variation is for the primary traits, grain yield under stress and unstressed conditions. However, variation for secondary traits such as yield components, especially kernel number per plant, and for the physiological components that contribute to the formation of yield under drought stress can speed progress for yield and allow the breeder to address key weaknesses in selections.

Figure 3. Hybrid x water stress interactions on a sandy soil in Hawaii in two elite temperate maize single cross hybrids with similar flowering dates. On this very light soil water was withdrawn for only two weeks starting 3 wk or 1 wk before 50% anthesis, and compared with a well-watered (WW) control (after Bruce et al. 2002).



Ultimately, however, the justification for measuring secondary traits must always be their contribution to improved grain yield under stressed and unstressed conditions. There have been many secondary drought-tolerance traits proposed, but ease of measurement does not justify their use. Useful traits are those that are correlated with yield under stress, cheap and fast to measure, highly heritable, stable in expression and not associated with yield loss under unstressed conditions (Barker et al. 2005). Relatively few meet these criteria. For maize those associated with grain yield under stress, in descending order of importance have been kernel number (barrenness; kernel number per ear), a short ASI; increased leaf erectness; reduced canopy temperature; and increased visual stay green and kernel weight (Bolaños and Edmeades, 1996). Where multiple traits are measured per genotype as well as grain yield, most breeders combine these data into a selection index or breeding value that heavily weights grain yield under stress and also includes unstressed yield to avoid loss of yield potential. Targeting of truly important traits during phenotyping, however, is still a work in progress (Passioura, 2012).

A second basic requirement for successful product development is access to a selection environment that lies within the target population of environments (TPE), but where stress intensity, timing and frequency can be reliably managed to expose genetic variation for traits season after season (Barker et al. 2005). Traditionally selection for stable yield has been through multilocation yield trials within the TPE, but drought in most maize TPEs is a randomly occurring event that gives rise to genotype x year interactions that are hard to interpret. Most drought breeders now prefer the "hotspot" approach, using managed drought stress environments (MSEs) -- rain-free testing sites that manage the timing and intensity of water stress though irrigation. The genetic correlation for grain yield between the MSE and the TPE should be positive and significant – something that should be tested as often as practicable. Increased interplant and interplot variability normally occurs under stress, and heritability of grain yield declines, so emphases on secondary traits and precision phenotyping are needed (Barker et al. 2005). Best practice calls for the standard use of statistical methods to remove spatial trends in data, but there is no substitute for careful selection and management of experimental sites. Well-irrigated control plantings are normally used to monitor changes in yield potential.

The need for high quality and high throughput phenotyping is increasing. Marker-aided selection (MAS) has helped reduce the volume of field testing, but the genotype-phenotype associations upon which MAS are based depend heavily on accurate phenotyping. This is especially the case when phenotyping training populations during genomic selection and when validating new genes and constructs. Nonetheless, the widespread use and rapid analysis of remotely sensed environmental and phenotypic data is allowing a steady increase in the volume of plots that can be evaluated for an array of current and new traits in real time (e.g., Araus et al. 2012; Berger et al. 2010; Masuka et al. 2012; Römer et al. 2012). New methods for the rapid evaluation of roots are emerging (Hund et al. 2010; Trachsel et al. 2011), and networks of managed stress testing sites at carefully chosen locations in the TPE are being established (Rebetzke et al. 2012). Phenotyping is catching up, but its precision, repeatability and speed still remain the bottleneck for the majority of genome wide association studies.

Models are becoming increasingly used as breeding aids. The combination of environmental and genetic data and crop and genetic models is now allowing the testing of genetic and physiological hypotheses *in silico* before a seed is planted (Chapman, 2008). Pioneer has developed advanced modeling capability of this type to support the development of drought tolerant products, for example AQUAmax (Messina et al. 2011), but still relies heavily on field testing as the final arbiter.

b. Product development in the public sector

Method development and validation: For the past 38 years CIMMYT has undertaken selection for drought tolerance in tropical maize using rain-free tropical locations and irrigation to create its MSEs. These studies have been extensively described elsewhere (Bolaños and Edmeades, 1996; Edmeades et al. 2000; 2006; 2008; Bänziger et al. 2006; Monneveux et al. 2006). In summary, recurrent selection using an index of traits was conducted for 2-9 cycles in six improved tropical populations, normally evaluated under well-watered and two distinct drought stress regimes in Mexico. Evaluations in multilocation trials under optimal, water stress (70% yield reduction) and low N environments (31% yield reduction) showed consistent gains averaging 164 and 99 kg/ha/cycle under drought and optimal conditions. Barrenness and ASI were also reduced under drought (Table 1). Gains in drought tolerance from selection under MSEs were significantly greater than those from selection in similar populations under multilocation testing alone. Gains transferred well to other environments such as moderately low N (Table 1; Bänziger et al. 1999), and showed only moderate levels of G x E. This suggests that selection resulted in a constitutive change in floral behavior and reproductive efficiency through changes in biomass partitioning to and within the ear (Edmeades, 2008). Importantly, it became clear that improvements in performance under drought stress carried no penalty for yield under optimum conditions, and there was no evidence of negative correlations between the two.

Table 1. Selection gains in six tropical maize populations. Four were evaluated at 3-6 water stressed (SS) sites, at 5-8 well-watered (WW) sites, or at two low N sites in 1992-4, and two (DTP1, DTP2) were evaluated at one low N, SS or WW location in 2002-3. Yields relative to unstressed levels were 30% under drought stress (SS) and 59% under low N.

Population	**Cycles selected**	**Yield**			**ASI**	**Ears plant^{-1}**
		SS	**WW kg ha^{-1} cyc^{-1}**	**Low N**	**SS d cyc^{-1}**	**SS no. cyc^{-1}**
La Posta Sequia	3	229**	53 ns	233**	-1.2**	0.07**
Pool 26 Sequia	3	288**	177**	207**	-1.5**	0.08**
Tuxpeño Sequia	8	80**	38**	86**	-0.4**	0.02**
Pool 18 Sequia	2	146**	126**	190**	-2.1**	0.05**
DTP1	6	160*	80 ns	210*	-0.6**	0.03**
DTP2	9	80*	120 ns	60 ns	-0.3**	0.01*
Mean Gain		**164**	**99**	**164**	**-1.0**	**0.04**

Symbols *, **, ns signify significant rate of change per selection cycle at $P<0.01$, $P< 0.05$ or $P>0.05$. (Edmeades, 2008; Monneveux et al. 2006).

Molecular breeding for improved drought tolerance in tropical germplasm began in the early 1990s at CIMMYT and has been strongly supported by the Generation Challenge Program. Initially it focused on identifying QTLs for key traits in progeny of biparental crosses, but the cross-specificity of QTLs and the absence of QTLs with large effects have rendered this approach of limited use. Proof of concept research showed that marker-assisted backcrossing of QTL from a tolerant donor to susceptible line improved performance under stress (Ribaut and Ragot, 2007) but the procedure with the marker technology available at the time was not cost effective. However, a maize consensus linkage map of key traits under drought, based on 40 evaluations of progenies from six tropical maize crosses, has been established (Ribaut et al. 2008), but shows large QTL x population interactions. Other meta-analyses of QTL have also identified consensus QTL for drought tolerance as well (e.g., Hao et al. 2010; Almeida et al. 2012). However, as noted by Bernardo (2008), the identification of distinct QTL has had little impact on public sector improvement for drought tolerance in maize. Furthermore, the detailed marker-assisted backcrossing needed to transfer the QTL is resource intensive and error-prone. Newer MAS breeding methods such as genomic selection minimize both of these issues.

Sub-Saharan African public sector programs: Based on the promising field results shown in Table 1, the locus of selection was moved to southern Africa in 1997 where the work was supported by a range of donors. Selection methods were modified to always screen under low N, drought stress at flowering and optimal conditions, and were applied in a regular pedigree maize breeding program, as described by Bänziger and Araus (2007). Emphasis was placed on grain yield and secondary traits whose heritability remained high under stress. National research programs also provided MSEs that were used to validate genetic gains obtained from testing in CIMMYT's key selection centers in Zimbabwe and Kenya. Initially there were large yield gains. CIMMYT-selected hybrids, when compared with current commercial hybrids from southern Africa across 36-65 sites, showed a 13-20% yield advantage in the 1-5 ton/ha yield range and a 3-6% in the 5-10 t/ha yield range (Bänziger et al. 2006).

The success of this approach led quickly to increased donor support. The Drought Tolerant Maize for Africa (DTMA) and the Water Efficient Maize for Africa (WEMA) Projects resulted --- both funded by the Bill and Melinda Gates Foundation for a 10 year period. The DTMA, initiated in 2007, involves CIMMYT, IITA and 13 national programs in sub-Saharan Africa. It uses conventional selection and MAS to improve germplasm adapted to the drier sub-Saharan maize environments. Phenotyping is concentrated in well-developed regional MSEs established in Kenya, Zimbabwe, Zambia and Nigeria. DTMA has focused around conventional pedigree hybrid breeding as well as biparental marker-assisted recurrent selection (MARS) schemes. The WEMA Project started in 2009, involves CIMMYT, Monsanto and five eastern and southern African countries, and has a conventional, MARS, and transgenic components. Drought is also an issue in Asia: currently there are two drought tolerance projects underway in South East Asia, both led by CIMMYT and funded by the GCP or the Syngenta Foundation, and involving India, China, Vietnam, Indonesia, Thailand and Philippines.

Molecular breeding is an integral part of DTMA and WEMA. DTMA has a well-characterized association mapping panel of 293 diverse inbreds that have been used to identify genomic regions and sources of tolerance to drought and heat alone or in combination that could potentially be used in a wide range of germplasm (Cairns et al. 2013). The authors noted that some drought tolerant source lines became susceptible as temperatures increased, pointing to the need to screen for tolerance to both stresses simultaneously.

It is noteworthy that 7 of the top 10 source lines in this study have come from populations selected solely for drought tolerance in Mexico – an indication of the role for source populations in which the frequency of stress tolerant alleles has been deliberately increased by targeted selection.

The MARS improvement schemes of DTMA and WEMA involve establishing marker-trait associations in the first cycle of phenotyping and using markers for the identified QTL to direct MAS in the following three cycles without further phenotyping. Large-effect QTLs accounting for more than 10% of the phenotypic variance have not been identified for drought tolerance in maize. MARS has therefore been modified to a form of genomic selection (GS) based on genome estimated breeding values (GEBVs). Recently CIMMYT has begun using up to 350,000 SNP markers based on genotyping by sequencing of 100 lines from each cross, and using these as training populations to impute the GEBVs of the remaining 100-150 families in each cross and to guide recombination for the next three cycles. However, already DTMA and WEMA have created a unique database comprising 5000 lines from 27 inter-related populations that provides an excellent basis for genetic studies on drought tolerance in tropical germplasm, and will facilitate a flow of improved drought tolerant hybrids for several years to come.

Preliminary but incomplete estimates in sub-Saharan Africa of yield gains from conventional selection without markers reveal improvements of 39-80 kg/ha (or 1%) per year under optimal conditions, but only non-significant gains of 18 kg/ha (or 0.6-1.0%) per year under drought stress. Formal estimates of gain from the conventional breeding program and of MARS are currently underway. It is however apparent that gain under drought has been slowed by low heritability in regional trials and in trials under managed stress, often associated with soil variability, variable stands and managed levels of stress that are probably too severe. The need to select for disease resistance and broad adaptation has slowed progress for drought tolerance *per se*, yet is essential since these projects are producing finished products rather than drought tolerant sources. One key finding that will improve future testing efficiencies is a lack of significant G x E interaction for grain yield between eastern and southern African test sites. The ability to merge test site data across this region will result in improved heritability and genetic gain (Windhausen et al. 2012a).

Role of GWAS: There is broad general confidence among leading public sector maize researchers that the combination of doubled haploid (DH) inbred lines (see below) and genome-wide association systems (GWAS, essentially association mapping coupled with genomic selection) linked to precision field-based phenotyping, can double the current rate of genetic gain for yield and for drought tolerance as well. These techniques will undoubtedly be used much more extensively in the future since outsourced, rapid and cheap genotyping is now available, and high throughout phenotyping has made considerable progress (Bernardo, 2008; Lorenz et al. 2011; Yan et al. 2011). It is clear that the research community is learning how to use this technique since some authors have reported excellent predictive power from genomic selection (e.g., Crossa et al. 2010; Schussler et al. 2011) though others have reported far less success (Windhausen et al. 2012b). It is not surprising that the predictive power of a training population used to impute the GEBVs of other lines is greatest when the training population and lines are from similar genetic backgrounds, there is no hidden population structure among the lines, and when the training population and the predicted offspring are grown in similar environments (Windhausen et al. 2012b).

Heat tolerance: This has become a significant research area for CIMMYT maize scientists who have identified several excellent field screening sites (DTMA, 2012). Studies of grain yield under drought and/or heat stress show a non-significant relationship between them (Table 2), indicating that they can be improved independently. CIMMYT has recently announced a partnership with USAID, Purdue University, Pioneer Hi-Bred and several South Asia partners to develop and deploy heat tolerant high yielding hybrids for South Asia where an estimated 15% of hybrid maize area is vulnerable to high temperatures (https://www.agronomy.org/science-policy/sspr/2012-11-07/#2012).

Table 2. Genotypic correlations among grain yields of a common set of top crosses (Tester CML539 on 293 lines from the DTMA association mapping panel) assessed under drought (8 locations), drought with heat (3 locations), heat alone (1 location) and a well-watered control (6 locations) (Cairns et al. 2013).

	Drought	Drought + Heat	Heat
Drought + heat	0.08		
Heat	0.49	-0.07	
Well-watered	0.63	0.24	0.27

Transgenics in the public sector: Public sector efforts in delivering drought tolerance via transgenes in the absence of private sector partners are rare and at an exploratory level only. This is in part because of the costs involved in development and deregulation, and in part because of concerns about the complex nature of the trait.

The role of the public sector: Although public sector breeding for drought tolerance has contributed meaningfully to the development of methodology and the supply of improved source germplasm, when compared with the multinational maize seed companies it generally lacks the sustained resources, the critical mass of staff, and sometimes the discipline and coordinated action to develop a consistent pipeline of drought tolerant products over decades. Exceptions are the flow of improved drought tolerant hybrids developed in DTMA and through public-private partnerships such as WEMA, but their success will depend on continuity of funding and staffing, and strong links to the private seed sector.

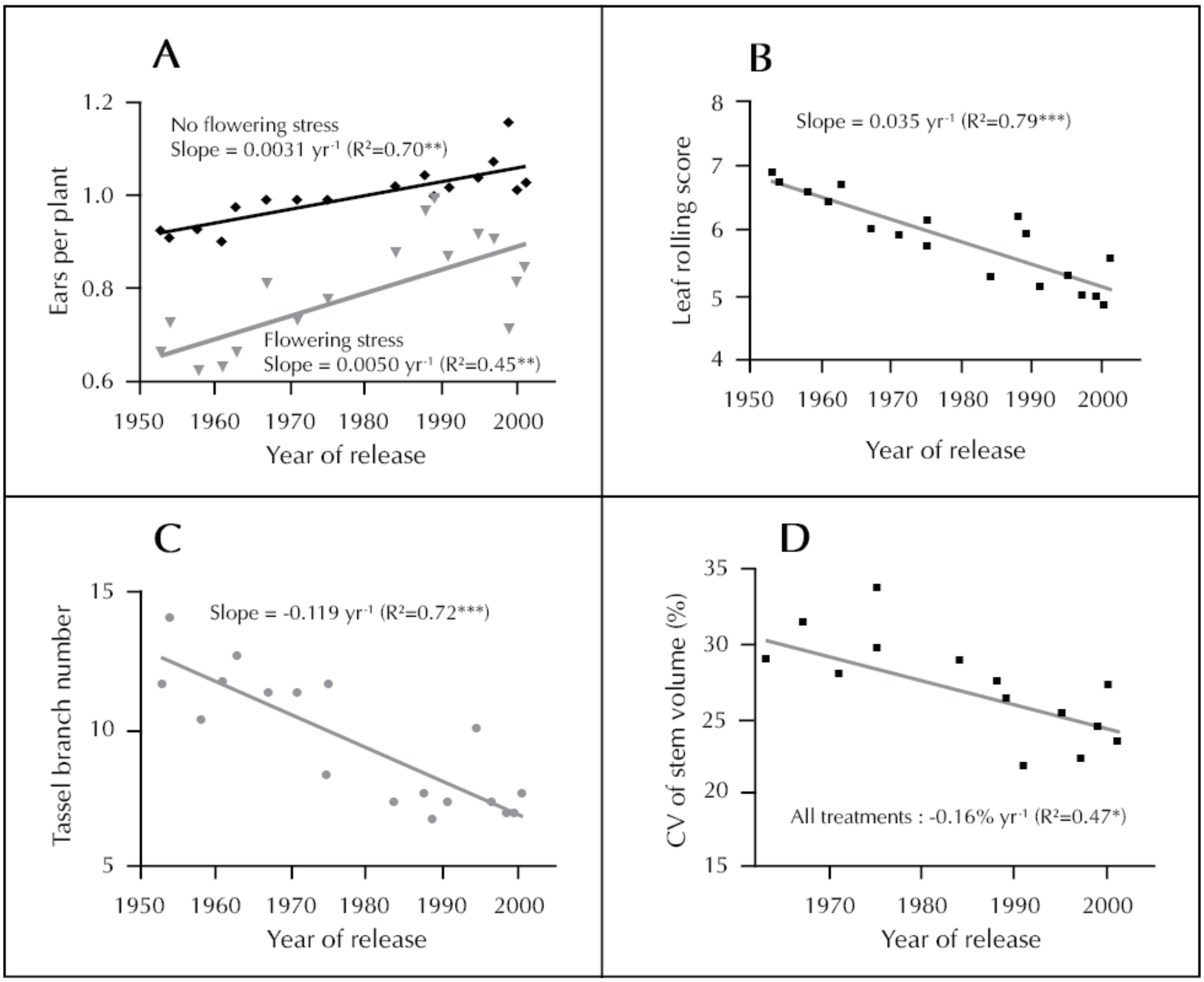
c. Product development in the private sector

Conventional: There has been significant improvement in drought tolerance in temperate commercial hybrids adapted to the US Corn Belt. The evidence for this is drawn mainly from hybrids developed by Pioneer, but older evidence points to a similar trend with DeKalb hybrids (Castleberry et al. 1984) and applies to most competitive temperate hybrids grown today.

We draw on results from a study of 18 elite commercial hybrids released in a time series from the mid 1950s through 2001 -- a subset of the full set of ERA hybrids studied extensively by the late Don Duvick (Duvick et al. 2004). All were developed through multi-location testing. Evaluations of changes in drought tolerance with time are described elsewhere in (Barker et al. 2005; Campos et al. 2006; Edmeades, 2008). Briefly these were evaluated in Chile over two seasons and subjected to drought stress at different growth stages from flowering to physiological maturity. This reduced grain yields by 36-71% compared to the irrigated control. Rates of gain in grain yield were greatest under unstressed conditions (196 kg/ha/yr), moderate under flowering stress (120 kg/ha/yr), and least (52 kg/ha/yr) in late-grain fill stress. Yield gains were accompanied by a decrease in ASI, an increase in kernels per plant, due mainly to reduced barrenness (Figure 4A) and less to increased kernels per fertile ear. As noted before (Edmeades, 2008), gains in weight per kernel and stay green were significant gain under irrigation but not under terminal stress, suggesting that in this circumstance kernels failed to fill fully under drought because of lack of current assimilate. Other changes, shown in Figures 4B-4D, show that newer releases rolled their leaves more readily, had much smaller tassels and greater plant-to-plant uniformity.

In a similar study of the full set of 54 ERA hybrids under drought at two densities in Woodland, CA, Barker et al. (2005) reported similar trends. In this study, stress was imposed only at flowering and throughout grain filling and was less severe than in Chile. Gains under irrigated conditions were around 50% those observed in Chile. Time to 50% silk was unchanged by year of release.

Figure 4. **Gains from selection in a time series of temperate hybrids grown under drought stress imposed at different growth stages; A: Ears per plant; B: Leaf rolling score where 4 is rolled and 8 is flat; C: Tassel branch number; D: The coefficient of variation (CV) of stem volume per plant (Edmeades, 2006; unpublished data).**

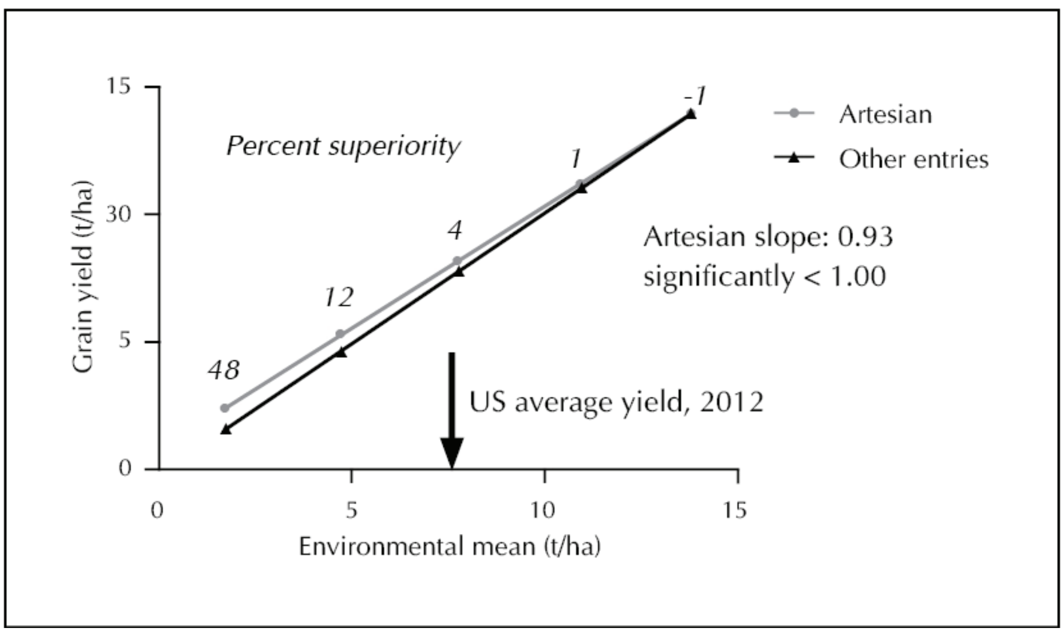


It is clear that progress in tolerance to drought at flowering has been made through selection based on extensive multi-environment trials. For example, in the Woodland study under drought imposed at flowering hybrids released in the 1940s (N=6) yielded 2.20 t/ha vs. 7.19 t/ha for hybrids from the 1990s (N=11), a 227% or 4.99 t/ha increase. Under grain filling stress the respective yields were 4.97 t/ha and 8.69 t/ha, a 3.72 t/ha or 75% increase, while under well-watered conditions they were 9.85 t//ha vs. 13.90 t/ha, a 4.05 t/ha or 41% increase. Gains were surprisingly similar across water stress levels in this study, but proportionally much greater for stress imposed at flowering. Improvements were almost exclusively through increases in kernel set under mid-season stress, initially from reduced barrenness and later from improved kernel set per ear. In a simulation study using similar data Hammer et al. (2009) noted that improved yields can only come from increased water capture in modern hybrids, something that they attributed to deeper rooting. The efficiency of applied irrigation water to generate grain has tripled from the 1940s to the 1990s through improvements in yield potential, increased water capture and drought tolerance (Butzen and Schussler, 2009). There is continuing evidence that drought tolerance in modern Corn Belt germplasm is linked to rooting volume and intensity (http://www.asgrowanddekalb.com/products/corn/Pages/rootdig.aspx). Field data based on evaluation the ERA hybrid subset suggest that conventional genetic variation for stay green under terminal drought stress (Edmeades et al. 2006) and tolerance of high temperature spikes at flowering and during grain filling may be insufficient to provide selection gains. These traits may ultimately depend on transgenic sources of variation for rapid change.

Molecular breeding methods show considerable promise for accelerating these historical gains – providing genetic variation is adequate. Eathington et al. (2007) and Edgerton (2009) have indicated that selection schemes similar to MARS have virtually doubled the rate of genetic gain in Monsanto's maize populations. Pioneer's "mapping as you go" presumably offers similar rates of increase in genetic gain in the context of a regular pedigree breeding program (Podlich et al. 2004). Association mapping and genomic selection have come more easily and quickly to the large commercial companies vs. the public sector because of their capacity to synchronize phenotyping and genotyping, massive capacity to field test mapping populations, extensive bioinformatics capability, and access to capital and elite germplasm (see Eathington et al. 2007; Edgerton, 2009; Schussler et al. 2011). In addition, the capacity for generating DH lines in large multinationals exceed 500,000 annually, significantly shortening the time for generating inbreds and improving the precision of comparison among lines and top crosses. The development of seed chipping methods allows DNA of DH lines to be assessed non-destructively, and undesirable DNA combinations are discarded – before ever being observed as plants. The combination of DHs, with seed chipping and genomic selection based on genotyping by sequencing or dense marker arrays has the potential to almost halve effect the generation interval and sharply increase the selection pressure, thereby "speeding the breeding" dramatically. The combination of these techniques, with a large increase in managed stress testing locations equipped with remote sensing capability for phenotyping means that genetic gains for drought tolerance may be more than double those from the 1930-2000 period (Edgerton, 2009).

Conventional native gene drought tolerant products: Drought tolerant hybrids selected using some or all of the above techniques have been available in the US market since 2011. Assessing performance is challenging in the absence of independent head to head comparisons. Yields of drought tolerant hybrids are often compared with an undisclosed list of "leading competitor hybrids" that may be several years old, and the comparison is certainly open to bias. Given this caveat, Syngenta's Agrisure Artesian™ hybrids, based on a series of 12 QTL that operate across a wide range of genetic backgrounds (http://www.freepatentsonline.com/y2011/0191892.html). Around half of these QTL have been obtained from non-Corn Belt sources. During the 2012 growing season when drought affected much of south and central US these hybrids Syngenta reported a significantly improved performance under severe stress (12% superiority in yields in the 3.1-6.2 t/ha range; 48% in yields less than 3.1 t/ha) (Figure 5). At yield levels of around 50% of potential (or 6.9 t/ha) the advantage is predicted to 0.4 t/ha or 6%.

Figure 5. 2012 yield of Agrisure Artesian™ hybrids in 1100 on farm strip trials in the US vs. an environmental mean comprising yields of control hybrids with and without putative drought tolerance. (http://www.syngentacropprotection.com/news_releases/)



A second company, Pioneer Hi-Bred launched a line of hybrids under the AQUAmax™ brand in 2011, developed from native gene selections using a QTL-based approach termed Accelerated Yield Technology™. This variant on genomic selection appears to use dense molecular maps, multilocation testing and markers as heritable covariates to focus on hotspots in the genome (Sebastian, 2009). It operates with DH lines whose top crosses are selected under managed stress environments. In 2012 extensive testing was undertaken in 3606 water limited and 7663 favorable environments. Over both 2011 and 2012 seasons side by side comparisons against competitive products show 8.9% superiority in water limited environments (less than 9.4 t/ha) and a 1.9% advantage in favourable growing conditions (greater than 11.3 t/ha) (http://www.4-traders.com/news/Pioneer-Hi-Bred-International-Inc). AQUAmax hybrids are characterized by vigorous silking and improved stay green. As with the Artesian hybrids and with the ERA hybrids described above, relative gains are greater under severe stress, and there is no yield penalty in optimum conditions. Artesian and AQUAmax hybrids will undoubtedly feature strongly in 2013 sales of both companies.

Although not identified under a brand name as such there is little doubt that Monsanto, DowAgrosciences and many other companies are developing conventionally-selected drought tolerant maize hybrids for the temperate market. Several have performed well in isolated trials against trademarked drought tolerant products (e.g., http://www.asgrowanddekalb.com/products/corn/pages/rootdig.aspx

Continued gains in public and private sector programs depend on the availability of adequate genetic variation, and faster rates of genetic progress may simply exhaust genetic variation more rapidly. New sources of genetic variation likely exist in germplasm collections, though these are hard to evaluate and utilize because of linkage drag from unimproved and narrowly adapted sources. Programs such as Seeds of Discovery, funded by the Government of Mexico, are providing advanced tools for identifying stress-tolerance alleles in CIMMYT's quite considerable germplasm collection (http://masagro.mx/index.php/en/components-en/seeds-of-discovery).

Transgenic drought tolerant products: As in 2008, a survey of published literature and of company websites was undertaken, but does not reveal the detail and extent of private sector investments in transgenic research for drought tolerance. The level of activity is gauged by public disclosures of a few leading companies. Drought tolerance is a genetically complex trait, so it is reasonable to expect that a successful transgenic strategy will rely on transcription factors and cascades of genes, or transformation with several transgenes affecting different but key processes. However, current attempts appear to be focused on single genes.

Monsanto remains the leader in transgenic research for drought tolerance in maize, and is scheduled to commence commercial sales of transgenic Droughtgard™ hybrids in 2013. The construct has recently been approved for sale for food and feed in the US and EU countries. Monsanto's event, MON87460, contains a cold-shock protein gene (*cspB*) isolated from *Bacillus subtilis*, a soil bacteria. The gene is thought to code for a protein that acts as a chaperone to other more stress-sensitive proteins such as RNA (Castiglioni et al., 2008), and although it appears be active throughout the life of the plant, its effect on yield is mainly by increasing kernel number per plant. The level of improvement it brings depends on the genetic background of the recipient hybrid and the environment. The complexities of this gene x genotype and G x E interactions have delayed its release as a commercial product. After the dry 2012 season Monsanto has indicated, based on over 2000 comparisons, that adapted hybrids carrying MON87460 provide 5 bu/acre (0.31 t/ha) yield advantage, or about 7% under drought that reduces yields by around 65% to 4.4 t/ha. In some genetic backgrounds its effect can be considerably greater than this (http://www.biofortified.org/2012/08/monsantos-gm-drought-tolerant-corn/). Its benefits appear to be from slowing growth (and hence water use), thereby saving water, maintaining photosynthesis and increasing kernel numbers per plant. It does not appear to reduce yields under unstressed conditions. This event is also on a deregulation pathway in South Africa, Kenya and Uganda. Additional classes of transgenes are under test by BASF and Monsanto who collaborate in this research. However, no obvious successor to MON87460 has yet been revealed. Meanwhile Monsanto continues collaboration in drought tolerance gene discovery, validation and delivery with BASF and with Evogene, an Israeli company specializing in computational genomics.

Other major seed companies are also pursuing transgenic drought tolerance in maize. Pioneer Hi-Bred have conducted an active research program on transgene-based drought tolerance for the past decade. Now all transgenes are compared with AQUAmax hybrids for effectiveness, and the commercial timeline, given in 2008 as potentially 2013, has been pushed out to further towards the end of this decade. Transgenes would need to complement the drought tolerance provided through AQUAmax to provide a "Stage 2" drought tolerance product. Pioneer has collaborated with Evogene and several other gene discovery companies in the past. Syngenta has a relatively smaller research effort in transgenic drought tolerance, and anticipate a commercial release in 2015. Syngenta signed a research agreement with Performance Plants Inc. for access to their YPT technology (see below) but the outcome of the collaboration is not known. Their testing sites under managed stress are significantly less developed than those of Monsanto and Pioneer. Dow AgroSciences is increasing its investment in native and transgenic sources of drought tolerance in their maize breeding programs (http://mobile.dow.com/news/press-releases/article/?id=6118), seeking to capitalize on their Smartstax® technology that allows insertion of up to eight transgenes simultaneously.

Other gene discovery companies generally license genes to the major maize seed companies to provide introgression, field testing and regulatory services. These include Bayer who is researching genes that reduce the drought-induced oxidant load that leads to tissue and DNA damage (e.g., RNAi poly ADP-ribose polymerase, or PARP). It is unclear how this product performs in maize and if there is commercial interest for maize. Performance Plants Inc. is a small Canadian company that patented its Yield Protection Technology (YPT) around 2006. YPT relies on engineered versions of farnesyl transferase genes that increase sensitivity to ABA thereby closing stomates rapidly when the plant stresses. YPT has shown good activity in canola and cotton, but only modest effects in maize under drought. Performance Plants also provides transgenes that are claimed to protect against heat and to enhance WUE. In the past it has had research agreements established with Syngenta and Pioneer, and claims that a drought tolerant variety of maize has been field tested for two years. Other candidate genes include members of the DREB/CBF transcription factor family (Yamaguchi-Shinozaki et al. 2006). These have shown efficacy at the seedling stage, but their value for increased grain yield in maize or wheat in the field has yet to be demonstrated.

There are many, perhaps thousands, of putative drought genes, but most have been found wanting. Many have shown some level of activity in seedlings or in greenhouses but have unacceptable levels of yield drag under unstressed conditions – a fatal flaw in a commercial hybrid. Others have failed when taken to the field and tested in real-life situations in full-sized plants that are flowering and setting grain under stress. Some do not actually improve stress tolerance but merely delay the onset of stress in pots because their growth is stunted and their water consumption reduced (Lawlor, 2012). Very few have regulatory packages associated with them. As we noted in 2008, identification of commercial-quality transgenes that enhance both survival under drought and production under adequate water supply is a lengthy, tedious and expensive process. At that time it was felt that the success rate in identifying suitable candidate genes was bound to increase as genomics and computational biology began to deliver powerful new analytical tools. This does not appear to have happened to the degree anticipated, and few breakthroughs can be reported in 2012.

4. Product delivery: its hurdles and successes

Changes since 2008 in product delivery have been slower than those in product development, and will only be summarized here. In developed countries adoption will depend mainly on the prices of seed and grain, superior and stable yield under drought and competitive yield under unstressed conditions. Seed is easily available, and information on the benefits of the product is readily accessed. Risk is relatively small, and crop insurance schemes ensure that farmers rarely face ruin from drought.

In less developed countries, however, the distribution and adoption of drought tolerant hybrids and varieties remain major constraints to their use. Seed of improved hybrids is often difficult to obtain, and farmers often face levels of risk to family incomes and food security that dwarf those faced in the developed world. At the same time, resource poor farm families have very limited capacity to accommodate risk, even though they are fully aware of profitability considerations (Heisey and Edmeades, 1999). Sources of risk are many, but a major one is drought superimposed on already low yield levels. Access to credit at reasonable rates is another so the outlay of cash for hybrid seed and fertilizer at the start of the season is especially challenging. The greater the perceived risk from drought, the more likely the farmer is to use his own saved seed and fewer inputs. Farmers will therefore often resort to sowing an open-pollinated variety (OPV) or seed saved from last year's hybrid harvest, even though it can be demonstrated that the risks of crop failure can be reduced by exploiting heterosis in stress-tolerant hybrids (e.g., Betrán et al. 2003).

Private seed companies are the preferred means of distributing drought tolerant hybrids, provided sufficient profit can be made from hybrids marketed into lower yielding and risky drought-prone regions. Experience suggests that yields of greater than ~2 t/ha provide a reasonable return on the cost of hybrid seed that is being produced for sale as cheaply as possible (Pixley, 2006). Circumstances resulting in yields of 2 t/ha from a drought tolerant hybrid will often lead to yields of 1 t/ha or less in an unimproved farmer variety, so this becomes a win-win situation. The deployment of drought tolerance in the form of hybrids has many benefits. Commercial seed quality and seed treatments are generally better than those of home stored seed, thus reducing risk of failed plantings. The generation and sale of hybrid maize seed, as opposed to seed of OPVs, has provided the foundation for a viable and stable seed industry – an essential step in development of a stable seed industry. Public and private seed companies in less developed countries are hampered by a lack of trained staff and quality-enhancing competition, by credit constraints, a weak infrastructure for distributing and marketing product, and inappropriate seed policies. As a consequence the maize seed industry in much of sub-Saharan Africa is still unable to offer consistent and well-tested hybrid seed options to small-scale farmers. As noted in 2008, until mean yield levels increase substantially, there remains a need for a diversity of seed systems that deliver drought tolerant hybrids and varieties – including NGOs, Government agencies, Universities and private seed companies.

Transgenic drought tolerance is encountering additional adoption challenges in less developed countries, mainly because the regulatory framework is still evolving. Under the auspices of the WEMA Project, both MON87460 and MON810 (Bt insect resistance) are in the confined field trial testing stage in Uganda and Kenya, while attempts are being made to establish the legal framework for these trials in Tanzania and Mozambique.

a. **Public sector:** While CIMMYT and IITA maize breeding programs have fully adopted pedigree breeding systems for hybrid development, there is still some demand in sub-Saharan Africa for OPVs as an intermediate step to generate confidence among farmers. Such OPVs are easily developed within a pedigree breeding system. Distribution of OPV seeds can be by farmer to farmer transfer, and seed can be recycled for several generations without loss of performance. The Mother-Baby trial system has been successfully used in southern and eastern Africa as a means of generating farmer participation in selection, adoption and seed production (Bänziger and DeMeyer, 2002) resulting in outstanding drought tolerant OPVs such as ZM521, ZM409 and ZM523. The generation and distribution of OPV seed must be seen today as a transitional step to hybrid production and sales since the formation of a viable seed sector will depend ultimately on hybrids sold each crop season rather than OPVs sold only periodically. Thus a major goal of DTMA and WEMA Projects is to strengthen the emerging private seed sector. More than 100 seed companies operating in sub-Saharan Africa north of South Africa are actively participating in testing and marketing drought tolerant hybrids developed in collaboration with DTMA and WEMA. South Africa has a mature maize seed industry, and is now providing advice to emerging companies in the rest of the region.

   In the meantime, the DTMA Project has produced conventionally selected hybrids that are passing through the release process – 15 in Kenya and 6 in Uganda, as well as several OPVs in West Africa. WEMA has nominated 16 hybrids in Kenya, 8 in Uganda and 5 in Tanzania to National Performance Trials. There are several drought tolerant hybrids already released by collaborating private seed companies in the regions that contain all or some lines derived from CIMMYT's long involvement in the region. WEMA has developed a strong emphasis on licensing lines to private seed companies in eastern and southern Africa, and this will help adoption while strengthening the private seed sector. It is hoped that in the next 2-3 decades the whole process of hybrid development can be handed over to the private seed sector.

b. Private sector: Product delivery in the developed world is efficient and effective. The availability of information is perhaps excessive and a farmer has to choose carefully among products, using information from independent head to head comparisons, e.g., Iowa Crop Improvement Association Corn Performance trials (http://www.croptesting.iastate.edu/). The costs and time involved in developing and deregulating transgenes means that only the well-resourced companies can undertake this step, variously estimated to cost up to $100 M per gene.

In the less developed world, transnational maize seed companies (Monsanto, Pioneer, Syngenta, and to a lesser degree regional companies such as Pannar, SeedCo, Kenya Seed Company and Pacific Seeds) are represented in most of the larger, higher yield potential markets. They have an advantage over national seed companies in that they have extensive and well-resourced research capacity, have extensive networks of technology suppliers, and can transfer adapted germplasm from one country to another to reduce product development overheads. However, because transnational seed companies operate only in the larger markets in areas where yields are relatively high, there is a good opportunity for national seed companies to establish a market niche comprising smaller market segments, and meet real needs through a balanced portfolio of stress tolerant hybrids and elite OPVs. No matter what the size distribution of private seed companies may be, a healthy, expanding, diverse and profitable private seed sector is essential for the sustained improvement and delivery of drought tolerant hybrids to farmers in regions such as sub-Saharan Africa and South Asia. Programs such as PASS (Program for Africa's Seed Systems, see http://www.agra-alliance.org/what-we-do/seed/) are playing a leading role in strengthening the domestic private seed sector in sub-Saharan Africa.

c. Private/public partnerships: Partnerships between private and public sector research organization are a strategy often proposed but rarely executed. WEMA is an important joint venture of this nature involving Monsanto as the main technology provider, CIMMYT as the source of key phenotyping sites and adapted maize germplasm, and national programs and seed companies as partners in testing and delivery. The African Agricultural Technology Foundation (AATF), a Nairobi-based not-for-profit organization, serves as the implementing agency, and will spearhead efforts to ensure regulatory compliance of MON87460 in target countries. WEMA has completed its first 5 year phase, with a further 5 years approved. Monsanto, CIMMYT and national programs are working together on MAS and conventional selection, building on Monsanto's extensive capabilities in doubled haploid line generation, molecular markers and bioinformatics in germplasm supplied by CIMMYT from DTMA or donated by Monsanto.

Phenotyping is shared between CIMMYT and Monsanto. MON87460 and MON810 have been provided by Monsanto on a royalty free basis for use in Kenya, Uganda, Tanzania, Mozambique and South Africa – the latter under special circumstances to small-holders only. Monsanto is carrying a large proportion of the load in helping these national programs build a system to deregulate and introgress these transgenes into adapted lines from CIMMYT. As with temperate hybrids, it has proved challenging to find a suitable genetic background for MON87460, and this is made more difficult by testing which is limited to 1-2 confined field trial sites per country. The early hopes of a 15% boost in yields under stress from this transgene have been replaced with a more modest expectation of 10%. Nonetheless, impact from conventionally improved hybrids should be felt within the next two years as released hybrids are taken up, and should be substantial. South Africa will be the first African country to benefit from transgenic drought tolerance. The time line for release could be as early as 2015 and 2017 in Uganda and perhaps Kenya.

The WEMA partnership in eastern and southern Africa presents a unique and important opportunity to bring modern technology to address drought tolerance for the poor, and will help put in place the regulatory procedures needed to bring other transgenes to this needy region. Aligning the cultures of the collaborating institutions has taken time, but the synergistic benefits of wholehearted private-public collaboration are now being felt. Based on the WEMA model the Gates Foundation have supported a similar initiative, Improved Maize for African Soils (IMAS) that aims to combine N efficient conventionally selected lines with a transgene being developed by Pioneer Hi-Bred that will improve N use efficiency significantly. In both WEMA and IMAS an issue arises over the action of the transgene. In both projects the transnational private company will only supply transgenes that have been deregulated for use as food and feed in the US, Europe and Japan. Many transgenes have significant effects in very dry or infertile soils but carry some yield penalty in optimal conditions, thus rendering them unattractive commercially. While they would be very suitable for use by African farmers, African national programs could not afford the full deregulation package if not paid for by the US donor company. Despite challenges of this nature, private-public partnerships must continue to be fostered as a win-win proposition for national programs, private seed companies and most importantly the African farm family.

5. Onwards and upwards? The way forward

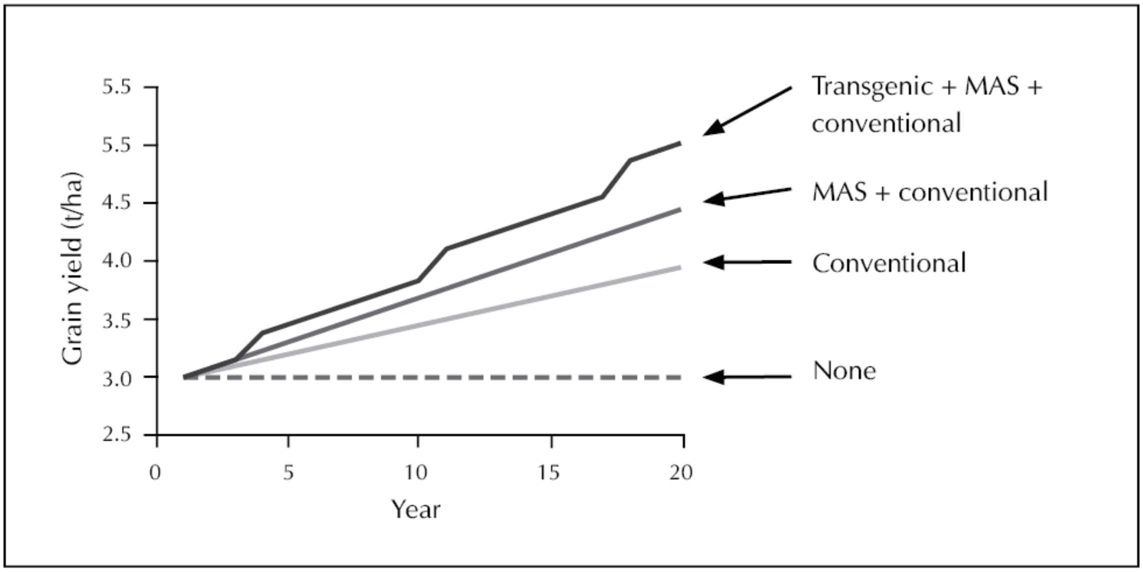
a. **Expected rates of gain in yield:** There is less optimism and more pragmatism in projections in 2012 vs. those of 2008. Published gains from directed selection solely for drought tolerance average around 100 kg/ha/yr

(Section 3b), but drought tolerant hybrids also require improved or maintained disease and insect resistance, stalk strength, correct maturity and appropriate grain quality. Estimates of realistic rates of gain under drought from conventional selection in a commercial context have therefore been reduced to 50 kg/ha/yr. Marker-assisted breeding, when well executed, can double gains from conventional selection (Edgerton, 2009), and successes with Artesian™ and AQUAmax™ hybrids generally support this contention. Rates of improvement from public sector MAS breeding in schemes such as DTMA and WEMA are still being measured, but there are challenges in managing genomic selection in real time in the less developed world. The increased rate of gain of [MAS + conventional] over conventional selection alone have accordingly been dropped to 50%.

The results from transgenic drought tolerance have also been reduced. Gains from MON87460, with some unique exceptions, now look to be 5% across a range of genetic backgrounds and the delay in announcements of new drought tolerance transgenes and timelines for commercialization by major companies speak for themselves. It is assumed that a realistic assumption would be a new transgene providing 5% yield gain every eight years rather than the 2008 assumption of one new gene giving 15% boost in yield every five years. Gains from each interventional are built on a base yield of 3 t/ha – a level considered and average for drought affected maize in temperate and tropical production environments. It is assumed that gains from each technology are additive (Figure 6), and this results in annual average gains of 50, 75 and 106 kg/ha/yr under conventional, [conventional + MAS] and [conventional + MAS + transgenics], or rates relative to mean yields of 1.4, 2.0 and 2.7% annually. This gives an average additional gain due to transgenes of around 30 kg/ha/yr – a figure which new technologies may well double in the future.

Thus, in resource intensive programs such as those conducted by multinational seed companies, these rates should be somewhat greater. Historical rates of increase in yield under managed drought in Pioneer's ERA hybrid set are reported as 72 kg/ha/yr (Schussler et al. 2011), so directed selection with MAS may well double this rate of gain in this germplasm. However, in general, going forward it seems wise to depend on rates of improvement under drought of around1-2%/yr and 50-80 kg/ha/yr in less well resourced breeding programs that address needs of whole regions where rates of gain are slowed by G x E interactions.

Figure 6. **Projected cumulative yield gain over a 19 year period in maize being selected for drought tolerance using conventional selection methods (50 kg/ha/yr), [marker-aided selection (MAS) + conventional] (75 kg/ha/yr) and [One transgene introduced every 8 years + MAS + conventional]. Each transgene added boosts grain yield by a cumulative 5%. Effects of each intervention are considered additive.**



b. **Role of the private, public and private + public sectors:** The public sector has played a large and important role in refinement of techniques, proof of concept, improved sources of drought tolerance, and germplasm collections to provide future genetic variation. This has been boosted by the substantial investment of the Gates Foundation and the 38 year leadership of CIMMYT in developing and disseminating drought tolerant maize (Bänziger et al. 2006). These roles should continue in areas where the private sector is poorly developed, and for clients in risky and low yielding environments. Research of this nature is a relatively slow process. Hybrids take 7-15 years from the initial cross to the onset of adoption, so a program that consistently delivers drought tolerant hybrids requires committed resources over several decades to be successful – something that is difficult to accomplish in the public sector today. To accelerate the process using MAS, the latest marker technologies, DHs, transgenes and bioinformatics requires substantial investments to reach a critical mass, something rarely found today in the public sector. A decade-long investment of US$3.5 billion in genetically modified crops by China is an example of this commitment (Stone, 2008). With this exception, public sector investments are dwarfed by those made in the private sector.

As the need and opportunity arise to speed up rates of gain in maize, the public sector must form alliances with the private sector, or allow the private sector to take over a large part of the MAS and genetic modification responsibilities this will entail. By so doing the development of the crop is linked to an efficient and sustained distribution sytem and market forces will dictate the research. Clearly the public and private sectors need to combine efforts based on their relative strengths, and this will require clear leadership and clear benefits for all partners involved, without overlooking the poorest of poor families in low yielding risky rainfed environments. A careful analysis of the factors leading to success of projects such as WEMA and DTMA is needed so we learn from these very important initiatives and replicate their success. The Standard Material Transfer Agreement (SMTA) administered by FAO that governs the level of royalties paid to countries to which the germplasm originally belonged will affect the willingness of some private seed companies to use CIMMYT germplasm. The impact of this royalty charge on the commercial use of CIMMYT germplasm is not yet known.

c. **Centers of excellence in phenotyping, product development and delivery:** The value of MSEs for efficient drought selection in maize has been consistently demonstrated over the past 20 years (Bänziger et al. 2006) and has been adopted by leading commercial companies as well. For less developed countries long term funding to maintain and expand existing publicly funded regional centers of excellence in phenotyping for drought tolerance, such as that at Kiboko, Kenya, seems fully justified. A similar argument can be made for regional centers to generate DH lines (recently approved by Gates Foundation) and for foundation hybrid seed to meet the needs of smaller seed companies and public national breeding programs. Public funding used in this way must be considered transitional en route to a full cost recovery and eventual privatization of each of these functions, though this may be several decades away.

d. **New genetic variation – the role of transgenics:** Although there has been a an apparent slow down in the number of drought-related transgenes coming to market over the past four years, this should be considered temporary. The identification of genes with small effects on drought tolerance continues at a rapid pace. Methodologies such as Smartstax® that allows up to eight transgenes to be located together ("stacked") so they segregate as a block, suggests a multigene approach to drought tolerance may be feasible. The capacity for addition and deletion of transgenes to or from specific genomic locations is rapidly improving. Small RNA fragments are emerging as powerful control elements of stress response in plants (Sunkar et al. 2007).

The promise of transgenic technologies is, however, being threatened by uncoordinated over-regulation. Unfortunately the biosafety framework leading to ordered testing and deregulation in sub-Saharan Africa is being developed country by country when a regional approach would be a far more efficient use of resources. Present systems are modeled on risks that experience suggests are overestimated. They are onerous and expensive to implement, and beyond the reach of the vast majority of institutions in the less developed world. James (2011) considers the lack of appropriate science-based cost- and time-effective deregulation based on actual risks involved is the most important constraint to the deployment of genetically modified crops. The recent ban by the Government of Kenya on the sale of genetically modified food (http://allafrica.com/stories/printable/201211301197.html), and the introduction of strict liability for developers and users of GM crops in Tanzania are both slowing the use of this important technology under the pretext of the need to gather more information on its risks. Thus the precautionary principle on transgenic crop regulation in its present form is hurting resource-poor farm families -- the very people it was designed to protect, and forcing the development of transgenics back into the hands of a few large well-resourced institutions.

e. **Agronomic interventions:** Improved crop management methods can complement the use of drought tolerant hybrids and contribute significantly to increasing and stabilizing yields under rainfed conditions or under irrigation where water supply is limited. Conservation agriculture, a collection of practices embodying the use of reduced or zero tillage and mulch to reduce evaporation of soil water, is an obvious means of increasing water available to the maize crop (Thierfelder et al. 2012). The use of plastic mulch in dry cool areas on the Loess Plateau of China has markedly increase WUE in maize (Fan et al. 2005). Drip irrigation can also reduce evaporative losses and deficit irrigation can increase WUE, often at little cost to yield (Fereres and Soriano, 2007).

6. Conclusions

As in the 2008 review, it is clearly possible to improve drought tolerance at no cost to yield under optimal conditions. There is an increasing interest in drought tolerance, and the trait can be improved relatively easily in maize. The use of representative managed stress environments is again endorsed, as well as the ongoing need for public private partnerships. The requirement for sustained investment in drought tolerance, given the 7-15 year cycle for hybrid development, is strongly endorsed.

Other issues that have changed in importance since 2008:

- Genetic gains from manipulating native genes can only increase in the future. There has been a large increase in genome-wide association studies and the emergence of practical methods for genomic selection, meaning that native gene variation can be exploited more rapidly. Nakaya et al. (2012) state that although genomic selection is not perfect it is becoming a potent and valuable component of plant breeding. In the short-term gains in drought tolerance will come largely from native genes, and this will increase the need to identify new alleles that can sustain these. Germplasm collections are assuming greater importance.

- The transgenic route to drought tolerance has proven more difficult than first hoped. This is mainly because of the lack of genes with large effects, yield drag, gene x genotype and G x E interactions, and the decentralized nature and expense of the regulatory process and its enforcement in sub-Saharan Africa. In practice this mean that genes with small effects and limited market value are quickly abandoned.

- Tremendous progress has been made in the past four years in developing drought tolerant products – both in temperate and in tropical maize. The 2013 season will be a signal year – with Droughtgard™, AQUAmax™ and Agrisure Artesian™ hybrids on the market, and a large number of drought tolerant hybrids going through the release process in sub-Saharan Africa.

- Solid progress is recorded in regional approaches to developing drought tolerant germplasm in sub-Saharan Africa and in south Asia. If these regional initiatives and harmonization of regulations can be extended to release of improved hybrids and the deregulation of transgenes, these regions could see rapid development in their agricultural sectors.

- Efficient and accurate phenotyping is essential. While considerable progress in remote sensing methodologies has been observed over the past four years, in sub-Saharan Africa the need is simpler – trained support and effective mechanization of basic plot operations.

- Heat stress is receiving considerably more research attention, and although heat and drought often occur together, tolerance to each appears to be independent of the other.

- Selection for drought tolerance depends on dedicated staff who will stay in the field in the heat. They need to be adequately trained, supported and encouraged, then left to do what they do well, without institutional distractions that are so common in the developing world.

- The climate is changing, and the need for stable stress tolerant crop varieties and hybrids has never been greater. The tools and germplasm currently available, and the emerging private-public partnerships in crop development will be more than adequate to meet this challenge as long as our resolve does not falter and we use our resources wisely.

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