Abiotic Stress-resilient Maize for Adaptation to Climate Change in the Asian Tropics

P.H. Zaidi*, K. Seetharam, M.T. Vinayan, P. Nagesh, Raman Babu and B.S. Vivek

International Maize and Wheat Improvement Center (CIMMYT-Asia Regional Maize Program), ICRISAT Campus, Patancheru-, Hyderabad, India.
*Corresponding author; Email: phzaidi@cgiar.org

Introduction

Maize has emerged as the cereal with the largest global production. It surpassed rice in 1996 and wheat in 1997 and its production is increasing at twice the annual rate of rice and three times that of wheat (Fischer et al., 2014). Asia harnesses 28 percent of production, making it the world's second largest maize producer. Among the three major cereals in the Asian region, maize has recorded the highest increase in area and productivity in both South and Southeast Asia since 2000 (Figure 1). During this period, maize production doubled in both South- and Southeast Asia. (Figure 2).

The demand for maize exceeds global production. Forecasters predict that global demand for cereals by 2020, will increase 45 percent (compared with 30 percent for wheat and 32 percent for rice). Increase in maize demand is projected to be acute in Asia where an 87 percent rise in demand is expected by 2020 compared with its demand for maize in 1995 (IFPRI, 2003). Within Asian countries, demand is driven by countries of East Asia, dominated by China which alone would require 252 million metric tons (MT), followed by Southeast Asia requiring 39 million MT and South Asia 19 million MT (James, 2003). This has particular implications for Asia, where an array of factors contributing to a sharp increase in maize demand, including growth rate in per capita gross domestic product (GDP), changing diets and a significant rise in feed use for a rapidly growing poultry sector (Shiferaw et al., 2011). By 2020, the global area of maize is expected to increase by only 12 percent as compared to maize area in 2000. Thus, 88 percent of the necessary increase in maize production will have to be met from increased productivity per unit area of land (James, 2003). Meeting the projected maize demand is a daunting challenge for developing world maize farmers, who represent about two-thirds of the global maize area.

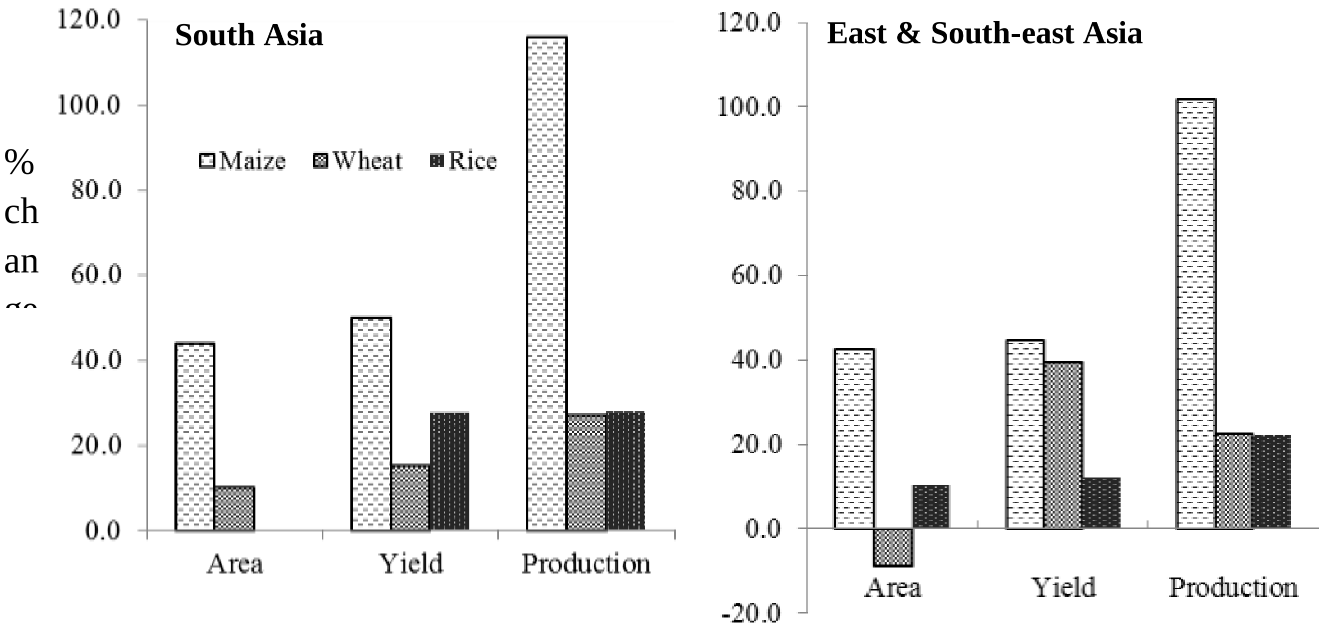


Figure 1. Gains (% increase) in area, productivity and production in three major cereals in Asia during 2000 to 2013 (FAOSTAT, 2014, Aggregate values).

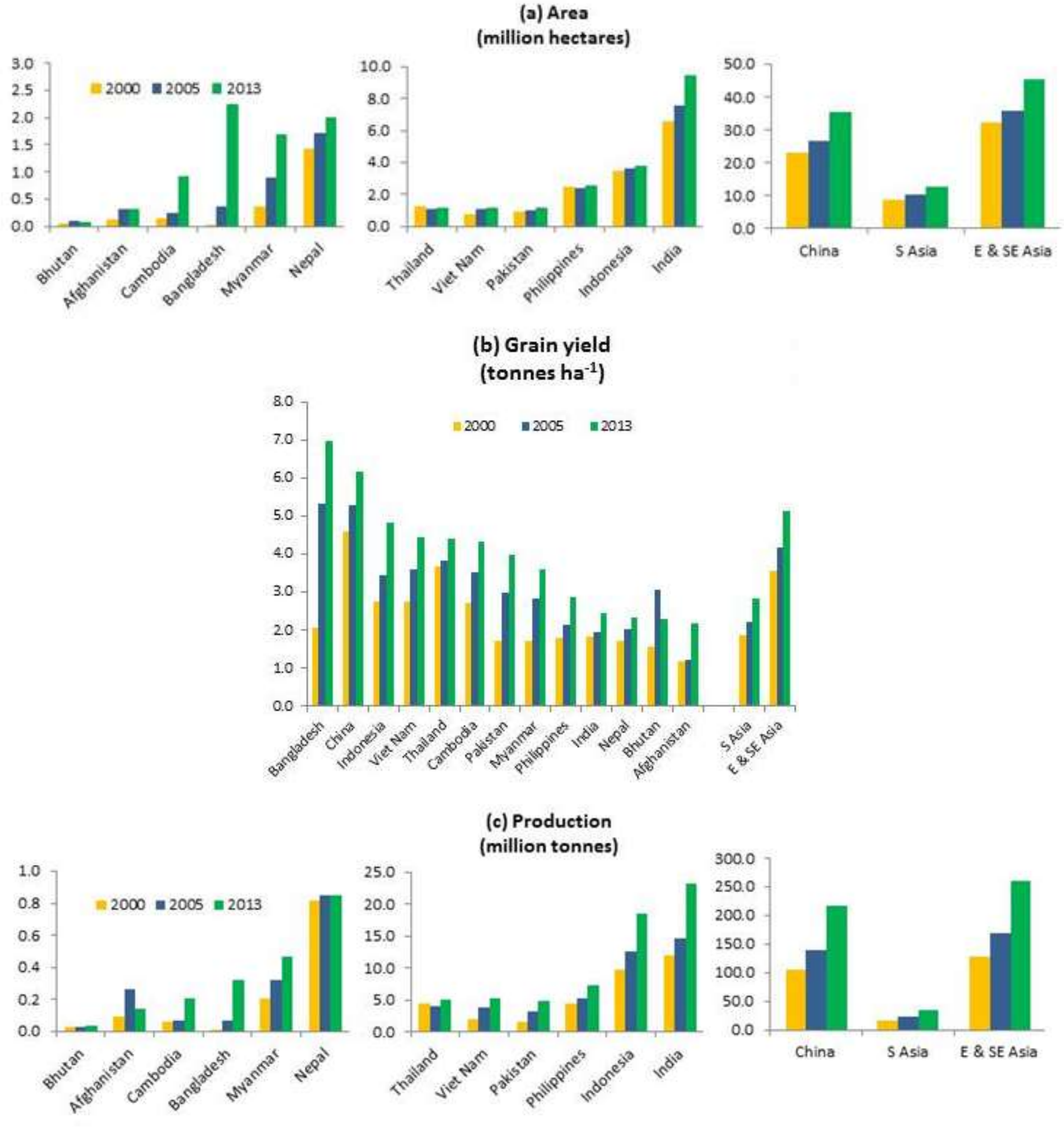


Figure 2. Growth in maize area (a), productivity (b) and production (c) in South and Southeast Asia during 2000-13 (FAOSTAT, 2014, Aggregate values)

Maize in tropical Asia -- a challenging environment

Broadly, there are six maize mega-environments across South and South-East Asia (excluding the temperate part of China [Figure 3])). Most of the maize in Asia (about 70 percent) is grown in lowland tropics (<1000 meters above sea level [masl]), including both dry- and wet-lowlands, followed by sub-tropical, mid-altitude and tropical highlands. Maize is largely (about 80 percent) grown as a rain-fed crop (Figure 4a), which is prone to hazards of monsoon rains which present an array of abiotic and biotic constraints. This impacts the productivity of the rainfed system, which is usually less than half of the irrigated system (Figure 4b). The rainfed maize area is projected to increase at a rate of 1.8 percent per year, six times the projected rate of increase of irrigated areas (Edmeades, 2007).

Generally, there is considerable pressure on irrigation, resulting in increased irrigation intervals that will subject the maize to stress and consequently, reduced yields. Moisture availability is seldom adequate for rainfed maize. Erratic, un-even distribution pattern of monsoon rains occasionally causes drought or excessive moisture and waterlogging at different crop growth stage(s) within the same crop season, which is probably the main factor responsible for relatively low productivity of rainfed maize (Figure 4b). Due to the uncertainty of assured returns, farmers are often hesitant to invest in recommended cropping management practices, therefore, low soil fertility results in un-met yield potential. Declining soil fertility and multi-nutrient deficiency is seriously affecting maize production in many parts of tropical Asia, especially in upland, sloping or hilly areas, which comprise major parts of maize growing areas in the region. Pressures from intensified land-use, minimal scope for fallow period, soil erosion and low soil fertility, limits further expansion of maize in marginal areas.

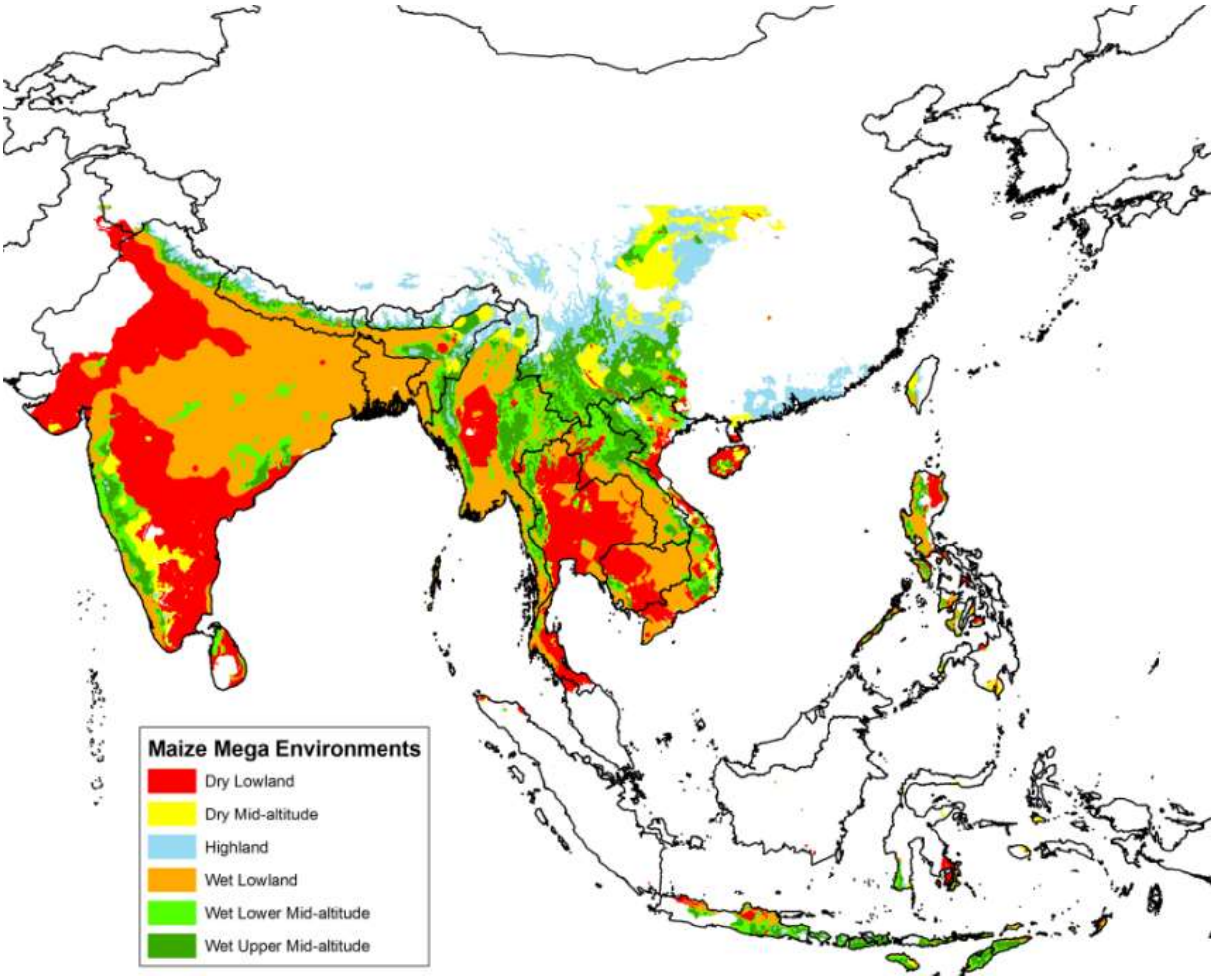
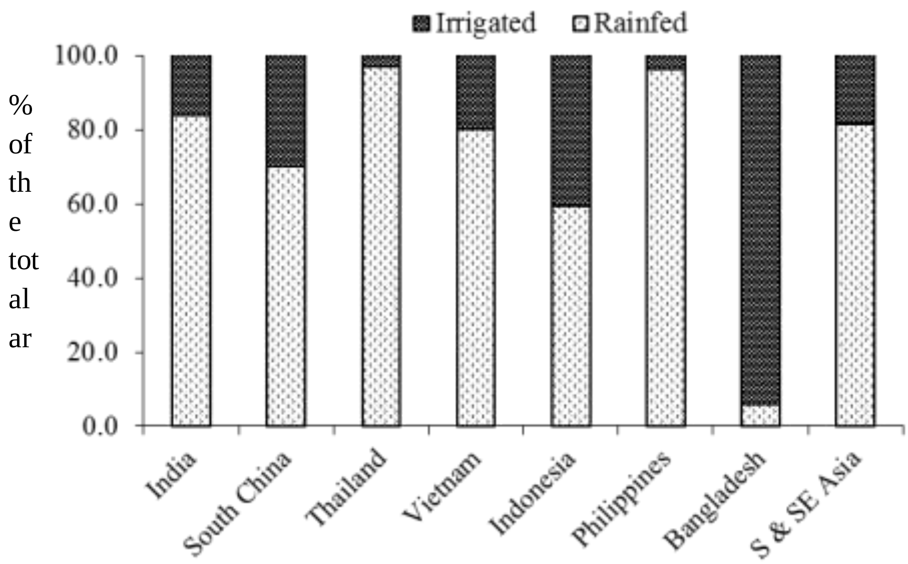
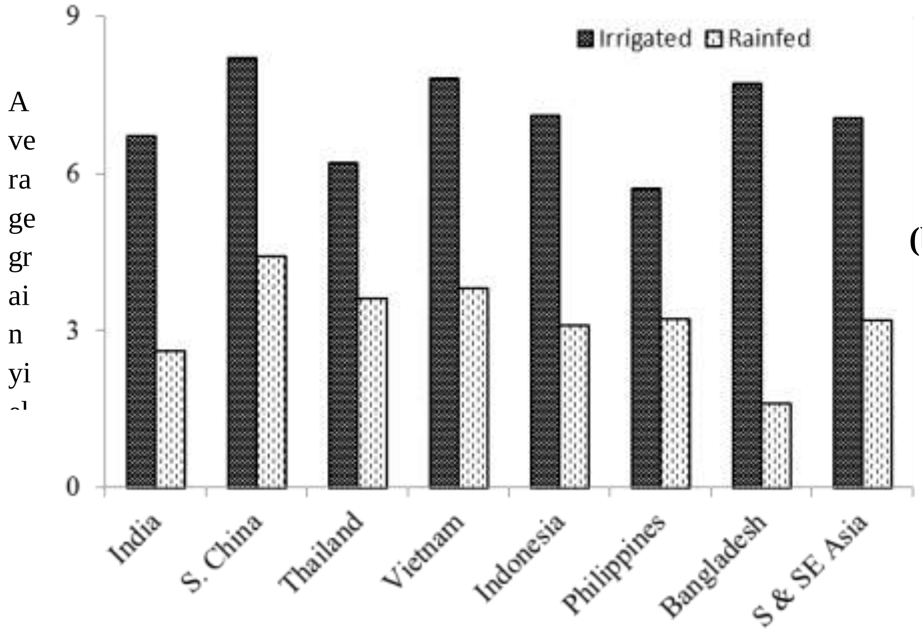


Figure 3. Maize mega-environments within South & South-east Asia (adapted from Hodson *et al.,* 2002).



(a)



(b)

Figure 4. (a) Maize production systems in Asian tropics, and (b) their average productivity.

Lowland tropics, especially wet-lowlands, are most condusive to biotic stresses, including diseases and insect-pests. The most common foliar pathogens in Asian maize, *Exserohilum turcicum*, *Helminthosporium maydis*, *Puccinia polysora* and *Pernosclerospora* have considerable economic impacts. Though reasonable sources of resistance to these diseases exist in Asian maize germplasm, new invasive species and the evolution of more virulent strains of diseases are posing a major challenge to the longevity of resistance. Therefore, host-plant resistance breeding programs require close surveillance of virulence changes in existing pathogens and identification of new resistance sources to new virulent strains. Banded leaf and sheath blight (BLSB) is emerging as a major threat in many parts of the Asian tropics, especially in the area where the rice-maize system lacks good sources of resistance to BLSB. Maize, in the Asian tropics, is prone to several stalk rots caused by range of causal organisms. *Stenocarpella* ear rots are common, but *Fusarium* and *Aspergillus* ear and kernel rots are also found, especially after a dry spell or insect attack and often leads to dangerous levels of mycotoxins in the grain. Stem borers, including *Ostrinia furnicalis, Sesamia inferens* and *Chilo partellus*, are widely distributed in Asia. Although some partial resistance to these pests exists, resistance is largely dependent on infestation load.

Climate change – a challenging environment further challenged

Climate change is threatening food production systems and therefore the food security and livelihoods of billions of people in Asia who depend on agriculture. Rainfed systems, dependent on prevailing weather conditions, are vulnerable to the effects of climate change. Asia tropics will experience an increasing frequency of extreme weather conditions with high variability beyond the current capacity to cope (ADB, 2009; Cairns et al., 2012). Several climate modelling studies suggested sharper increases in both day- and night-time temperatures, which could adversely impact maize production in the tropical regions (Cairns et al., 2012). Such impacts are already being felt in a number of real and recognizable ways in the region such as shifting seasons, higher frequency of extreme weather events, rising temperatures, more frequent drought, excessive rainfall and flooding, coupled with emergence of new and complex pathogens and insects.

In Asia, the effects of climate change include a reduction in the number of rainy days (although there has been no significant change in total rainfall) in South (Kashyapi et al., 2012) and Southeast Asia (Manton et al., 2001). Heavy rainfall events within a reduced number of days and extend the dry periods between rainfall within a cropping season, with erratic distribution of monsoon-generated rains results in waterlogging at some crop stage(s) and drought periods at other stages. The unpredictable trend and occurrence of more than one stress within the same cropping season, such as drought and heat stress, drought and water-logging, may increase the likelihood of short-run crop failures and long-run production declines, unless concerted measures are taken. Resulting food scarcity will lead to higher prices and reduced caloric intake across the region. Overall, the immediate and long-term impacts of climate change threaten social and economic progress in Asia.

Stress-resilient maize – a strategy for meeting current demands and addressing progressive climate change effects

Producing enough food to meet the demand of an increasing population with changing food consumption patterns, combined with diminishing resources and a changing climate scenario, is a challenging task for Asian farmers. Asian agriculture must become more productive, more resilient and more climate-friendly. Varieties with increased resilience to abiotic and biotic stresses will play an important role in autonomous adaptation to climate change (Fedoroff et al., 2010). Millions of small-holders in Asia grow maize under climate-vulnerable, rainfed conditions for their subsistence and livelihoods making the availability and access to climate resilient cultivars essential for food security.

To increase maize production, it is important to increase the availability of genetic diversity which harbors favorable alleles for higher yield, biotic and abiotic stress tolerance (Prasanna et al., 2012). Maize varieties, with increased resilience to abiotic and biotic stresses, will play an important role in helping farm communities in tropical Asia adapt to climate change. Targeted crop improvement, aided by precision phenotyping, molecular markers and doubled haploid (DH) technology, offers a powerful strategy to develop climate change-adapted germplasm. However, given the time lag between the development of improved germplasm and farmers' adoption in the targeted region(s), it is of utmost importance that adaptive strategies are rapidly deployed in selected tropical Asian countries that are most vulnerable to changing climate (Cairns et al., 2012).

CIMMYT's Asian regional maize program, in partnership with public and private sector maize programs, focuses on the development of high-yielding stress-resilient maize germplasm and donors for complex traits, such as – drought, heat and waterlogging. Its goal is to develop suitable maize germplasm for current environmental contexts and maintain a rich germplasm product pipe-line to effectively address emerging challenges in the Asian tropics.

Prasanna et al. (2012) highlighted the following key factors for accelerated development and effective deployment of stress-resilient maize varieties:

- Carefully undertaken, field-based precision-phenotyping at several relevant sites as well as under technically-demanding managed-stress scenarios, both of which are often beyond the capacity of individual breeding programs.
- An understanding of the genetic architecture of the target trait(s), coupled with application of modern molecular breeding tools, including genome-wide association studies (GWAS), genomic selection (GS) and double haploid (DH) technology for rapid development of improved products.
- Effective partnerships with committed national programs and seed companies in the region for sustainable deployment and delivery of climate-resilient cultivars.

Precision phenotyping

Whether the breeding approach involves conventional or molecular breeding, high-quality phenotyping is the key to success for genetic improvement of targeted traits. However, in practice, even the basic principles of phenotyping is often (knowingly) compromised, which eventually results in less-than-expected success in a breeding program. In order to realize the true success of breeding program (or power of novel molecular breeding approaches), it is essential to appreciate the principles of phenotyping and apply the following practices:

Screening, evaluating or phenotyping?

Often, the terms screening, evaluation and phenotyping are interchangeably (and incorrectly) used. To clarify, these are different steps in a targeted breeding program to iDentify best performing genotypes (Bänziger et al., 2000).

Screening – The first step in the breeding process, involves the testing of a large number of segregating genotypes (or their descendants) which are tested in small plots with few replicates (or even perhaps no replicates at all) at few sites in a target environment and selection based on key trait of interest only (such as grain yield).

Evaluation– The second step in the breeding process, involves the selection of genotypes from screening using relatively larger plots, with more replicates and at several sites in a target environment. Selection is done on the basis of key traits of interest along with a set of key agronomic traits associated with the primary trait of interest.

Phenotyping – The third and last step in the breeding process, involves a detailed characterization of phenotype of test entries under well-defined conditions (for example – managed drought stress). The purpose of this step is to precisely study the overall phenology of the test entries, which is the foundation for establishing genotype-phenotype associations in a molecular breeding approach.

Managed stress environment

The quality of phenotyping data is defined by the precision of the phenotyping environment. Understanding the target potential environment and simulating similar but more precise and uniform conditions (managed stress) is a pre-requisite for generating useful phenotyping data.

Phenotyping sites need to be carefully developed on the basis of key information about the site, including:

- A minimum set of medium-term (past 10 years) weather data (daily maximum and minimum temperature, humidity, rainfall and sunshine hours);
- Soil type – physical and chemical properties;
- Cropping history of the site;
- Field levelling and irrigation & drainage facility.

The overall purpose of these managed stress trials is to simulate the targeted stress with desired level of stress intensity and uniformity at critical stages of crop growth, in a way that the available genotypic variability is clearly expressed and could be recorded.

Phenotyping criteria

Generally, the major trait of interest for farmers, is always grain yield; however, under abiotic stresses heritability of grain yield is usually low, whereas heritability of some secondary traits remains reasonably high and also the genetic correlation between those traits and grain yield increases significantly (Bänziger et al., 2000). Also, at times, selection only on the basis of high-grain yield under stress is misleading, for example – selecting a high yielding test entry with pro-longed anthesis-silking interval (ASI; >5.0 days). Such an entry is able to produce high-yield as it is complemented by the synchronous availability of pollen from other test entries in the trial; a luxury not available in a commercial crop. Similar situations can be found with other stresses, for example, an entry with severe tassel blast under heat stress could give a high-yield for the same reason listed above but would be a commercial failure.

In the case of molecular breeding projects, detailed phenotyping is essentially required to support the huge volume of genotypic information generated in order to discover the power of that valuable information. It might be helpful to dissect complex traits, like tolerance to abiotic stresses, into components, which can enhance understanding of the cascade of events involved in conferring tolerance and also adding value in genomic region discovery efforts. However, a secondary trait to be considered in phenotyping portfolio, it must comply with some basic requirements (Edmeades et al., 1998), such as:

- Significant genetic variability for the trait;
- Significant genetic correlation with grain yield in the target environment, i.e. relationship is causal, not casual;
- Heritability of the trait is higher than grain yield itself, i.e.- less affected by genotype x environment interaction;
- Trait should not be associated with poor yields under optimal conditions, i.e. – it must confer tolerance rather than avoidance;
- Rapid and reliable measurement, which is less expensive than measuring yield itself.

Recently, initiatives are underway to establish a field-based high-throughput phenotyping platform (HTPP). To increase the throughput, more detailed measurements of plant characteristics with better precision (Prasanna et al., 2012) in order to develop field-based HTTP using low-cost and easy-to-handle tools, so that it becomes an integral and key component in the breeding pipeline of stress-resilient maize.

Root phenotyping

Root characteristics play a pivotal role in overall performance under optimal conditions and also adaptation to various abiotic stresses. However, most often this important hidden-half of the plant is "knowingly" ignored due to the complexity involved in studying root structures and functions. Root characteristics are often assessed on the basis of some surrogates (for example - leaf rolling), which may not accurately explain the stress-response or adaptive structural and functional changes in roots under stress conditions. Understanding how roots respond (or adjust) to a stress and support in adaptation is crucial for developing stress-resilient genotypes. Several breeding programs for drought tolerance have resulted in a decrease in the weight of the root system (Bruce et al., 2002; Campos et al., 2004), which may be interpreted as selection for reduced root weight which may help in enhancing drought tolerance.

CIMMYT's new root phenotyping facility in Hyderabad, India is based on the lysimetric system, which provides a means to directly assess and quantify root traits and their dynamics under various growing conditions and allows high-precision phenotyping of various root traits. It facilitated the root study, moving from a static assessment of roots through time-consuming extraction and scanning, to a real-time measurement of water uptake, water use and an assessment of variation in roots under different growing condition in the rhizosphere. The lysimetric system is not new, but it previously lacked essential tools. Recent advances in high-precision weighing systems and information technology tools revolutionized its efficiency and effectiveness as a root phenotyping system.

The study used the CIMMYT Asia association mapping (CAAM) panel which involved selection of 396 diverse tropical maize lines that were phenotyped for various structural and functional aspects of roots. Significant genotypic variability was observed for various structural and functional traits root traits, especially under drought stress. Root functional traits, such as stress-period-water-use and transpiration efficiency, showed comparatively stronger relationship with total plant biomass and grain yield under drought stress (Zaidi et al., 2014). Structural traits, such as root depth and root-length density, were more important in the case of early maturing entries under drought stress. The study suggested that root functional traits, compared to structural traits, were more heritable and highly-correlated to performance of genotypes, under drought stress.

Developing stress-resilience in Asian maize

High-yields under optimal conditions (yield potential) and reasonably good yields under stress conditions (adaptation to stress), are not mutually exclusive. Therefore, the study focused more on improved-stable yields across stressed- and non-stressed environment (i.e. resilience, rather than just tolerance to a particular stress). This was achieved by defining the phenotyping and selection strategy across range of environments and selecting the progenies that are have high-stable-performance across stressed- and un-stressed environments.

Historically. large gains have been made in cereal production through conventional breeding (Evenson and Gollin, 2003), including improved stress-tolerance in maize (Zaidi and Cairns, 2011). Conventional breeding methods that rely on generating a large set of segregating progenies and selection on the basis of extensive phenotypic screening, have been effective, but less-efficient in rapidly improving tolerance to individual and/or multiple stresses. Tolerance to most of the abiotic stresses, including drought, heat and waterlogging is polygenic in nature and complex. To increase the efficiency of breeding pipelines, the CIMMYT-Asia maize program uses a combination of conventional (index selection, including key stress-adaptive secondary traits along with grain yield, rather than yield alone) and modern molecular breeding approaches, e.g. genome-wide association studies (GWAS), rapid-cycle genomic selection (RC-GS) and marker-assisted recurrent selection (MARS) in genome-wide selection (GWS). Apart from trait-based phenotypic selection, several molecular breeding projects were initiated for fast-tracking the germplasm development in stress-resilient breeding program. This strategy helped in developing an Asia-adapted maize germplasm pipe-line with enhanced stress tolerance for individual or multiple stresses, without any compromise in optimal condition performance.

Association mapping

An association mapping panel, involving over 400 inbred lines representing diverse pedigrees, called the CIMMYT Asia Association Mapping (CAAM) panel, genotyped the panel using 1536 (Illumina-Golden Gate), 55K (Illumina-Infinium) and GBS (Genotyping by Sequencing – around 700K SNPs) marker systems. The test-crosses of the panel were phenotyped across 34 locations in the Asian tropics, including drought – eight sites, water-logging – five sites, heat stress – nine sites and optimal moisture – 12 sites. Apart from this, each panel line was phenotyped for resistance to common foliar diseases, such as - *Turcicum* leaf blight (TLB), *Puccinia polysora* (southern rust) and also for sorghum downy mildew (*Peronosclerospora sorghi*). The study resulted in the following major outputs:

- Genome-wide association studies helped in identifying major genomic region associated drought, water-logging or heat tolerance (Babu et al., 2014).
- The identified genomic regions are being validated and further introgressed in elite, but stress-susceptible Asia-adapted maize inbred lines, with established commercial value, as they are already used as parents in some of the popular commercial hybrids in Asia.
- An accelerated backcross (BC) conversion approach using molecular markers and doubled haploid (DH) technology, will be undertaken for fast-tracking the development of elite heat stress tolerant maize hybrids adapted to South Asian environments.

While introgression of major genomic regions (identified through GWAS), is being executed, the large-scale robust phenotyping data helped in identifying highly promising donor lines for various complex traits (abiotic & biotic stresses) and a few "shelf-ready" hybrid combinations for individual stresses as well as a few hybrids, with stable performance across multiple stresses and unstressed environments (Figure 5).

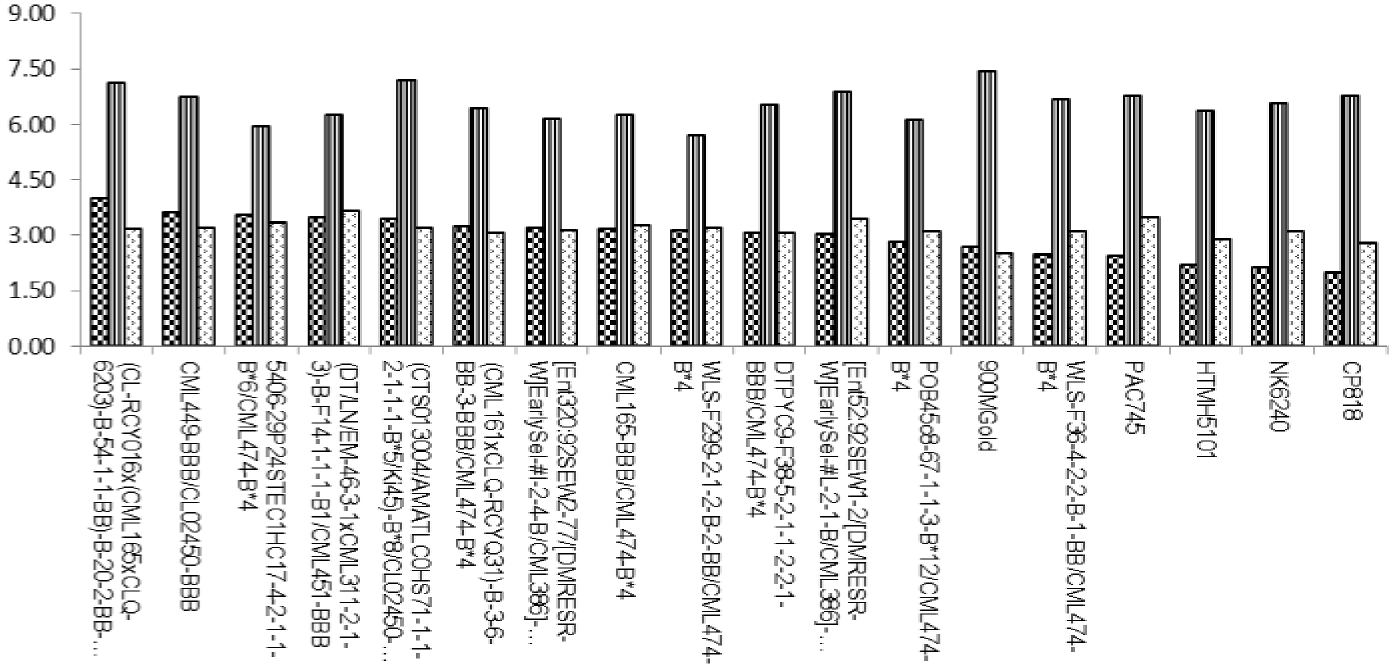


Figure 5. Stress resilient maize hybrids identified among CAAM panel test-crosses evaluated across several stressed and un-stressed locations along with commercial checks in the Asian tropics and their performance under drought (left bar), optimal moisture (middle bar and water-logging stress (right bar) (Genotypes. N = 862).

New generation of stress-resilient maize hybrids for stress-prone agro-ecologies

Experimental hybrids were developed by crossing promising lines with high-combining ability for individual stresses (tolerant x tolerant crosses, between heterotic groups). These lines were identified from the extensive phenotyping CAAM panel across a range of sites in Asian tropics and a few lines from previous studies. The experimental hybrids were evaluated across locations in a range of moisture regimes, including drought, water-logging and optimal moisture conditions. The top-ranking hybrids with high- and stable- performance across locations and moisture regimes were identified (Table 1) and available for immediate use in stress-prone agro-ecologies of tropical Asia.

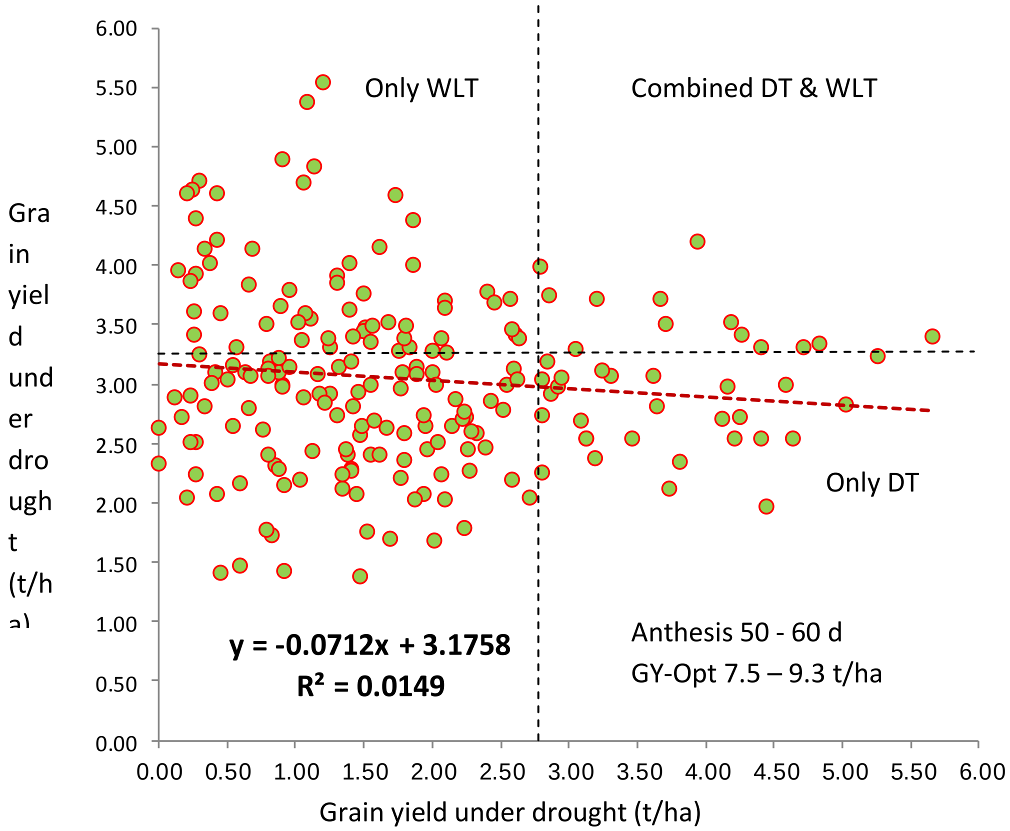
Table 1. Performance of CIMMYT's new experimental hybrids (tolerant x tolerant crosses, between heterotic groups) across 14 locations in Asian tropics under different moisture regimes.

Name	Pedigree	Grain yield (t/ha)_Across				
		Across_Opt. Anthesis (d)	Optimal	Drought	Water-logging	TLB (1-5)
Good across moisture-regimes						
ZH12112	WLCY2-7-1-2-1-5-B-2-3-1-2-2-BB/WLS-F310-3-2-2-B-1-BBB	53.5	8.37	2.53	4.71	2.3
ZH1250	POOL16BNSEQC3F22x1-3-2-2-2-BBB/CML444-1-BBB	53.9	7.46	4.26	4.31	2.0
ZH116072	[SYN-USAB2/SYN-ELIB2]-12-1-1-2-B*5-1-BBB/CML451-B	56.4	8.45	3.04	3.25	2.8
ZH12115	WLCY2-7-1-2-1-5-B-2-3-1-2-2-BB/CA00102-BBB-3-BB	52.7	7.46	2.85	3.04	3.3
ZH12111	WLCY2-7-1-2-1-5-B-2-3-1-2-2-BB/SO4YLWL-172-B-1-1-B-1-B	51.8	8.42	2.43	3.64	2.8
ZH1235	CML472-B/CA00106-BBB-5-BB	50.3	7.46	3.70	4.23	2.8
ZH111472	DTPYC9-F87-1-1-1-2-1-2-1-B*4/CML451-BBB	53.8	7.36	2.89	3.95	2.5
ZH111948	WLCY2-7-1-2-1-5-B-2-2-2-2-1-B*5/CML451-B*4	56.1	8.24	2.87	2.66	2.3
ZH12102	[SYN-USAB2/SYN-ELIB2]-12-1-1-2-B*5-1-BB/CA00102-B-3-B	50.3	7.87	2.89	2.73	3.5
ZH12101	[SYN-USAB2/SYN-ELIB2]-12-1-1-2-B*5-1-BB/CML433-BBB	56.1	8.41	2.16	2.88	2.5
VL1018145	CML442-B/POOL16BNSEQC3F28x15-3-1-2-2-BBB	51.1	7.46	2.20	4.00	3.3
900MG	Check-1 (900MG)	57.2	8.12	3.06	2.86	2.9
30V92	Check-2 (30V92)	53.4	8.43	2.69	2.55	3.3
Worst entry of the trial						
Z227-74	CL02450-BBB/CML451-BBB	57.5	6.43	0.63	0.96	3.0
	Mean	52.7	5.48	1.71	0.75	2.8
	LSD (0.05)	1.2	0.72	1.03	0.59	0.7
	MSe	0.5	0.77	0.27	0.13	0.1
	Min	50.4	5.20	0.63	0.80	2.0
	Max	60.8	8.45	4.26	4.71	3.8

New generation of stress-resilient germplasm for climate change adaptation

The most promising stress-tolerant lines for various traits are used in developing a range of new pedigree populations combining two stresses, such as drought- and water-logging, including both back-cross (BC) and bi-parental (BP) populations. These populations are used in both trait-based breeding and molecular breeding using genome-wide selection (GWS). More than 700 BC_1F_4 lines, derived from BC population, were developed using the most promising drought-tolerant and waterlogging-tolerant lines. Test-crosses of BC_1F_4 were evaluated across different moisture regimes, and this resulted in the identification of a new generation of drought- and waterlogging- tolerant lines, significantly superior to their parents and few unique lines with combined drought- and water-logging tolerance (Figure 6).

Bi-parental populations were generated from the crossing of an elite Asian-adapted yellow inbred with drought-tolerant donor lines (CML444) and improved using genome-wide selection (GWS). Marker effects of single nucleotide polymorphism (SNPs) were determined from the F_3 test-crosses. Cycle 1 was formed by recombining the top 10 percent of the F_3 families based on the test-cross data. In order to assess the selections gains, C_2 was derived from both phenotypic selection (PS) and genomic selection (GS) using high- genetically estimated breeding values (GEBVs). All the generations were evaluated under managed drought, which indicated that C_2 (GS) showed superiority (16.5 percent and 25 percent) over C_2 (PS) of respective populations (Figure 7). Thus, use of GEBVs enables the selection of superior plant phenotypes in the absence of the target stress and results in rapid genetic gains for drought tolerance in maize.



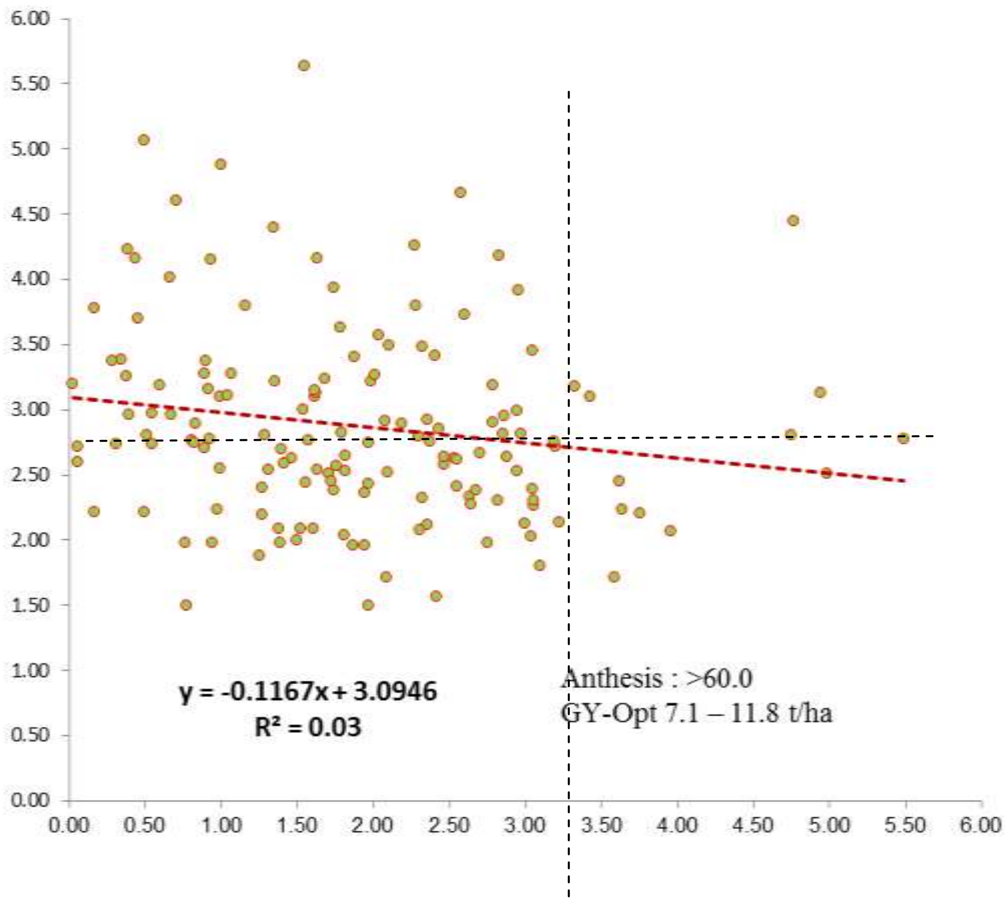
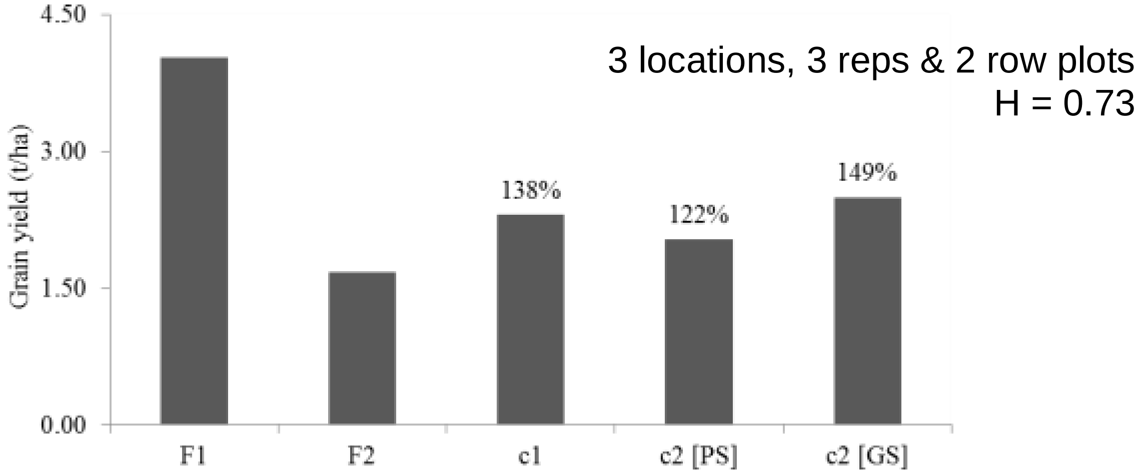


Figure 6. Performance of BC1F4 testcross of (drought x waterlogging) x drought back-cross populations under various moisture regimes.



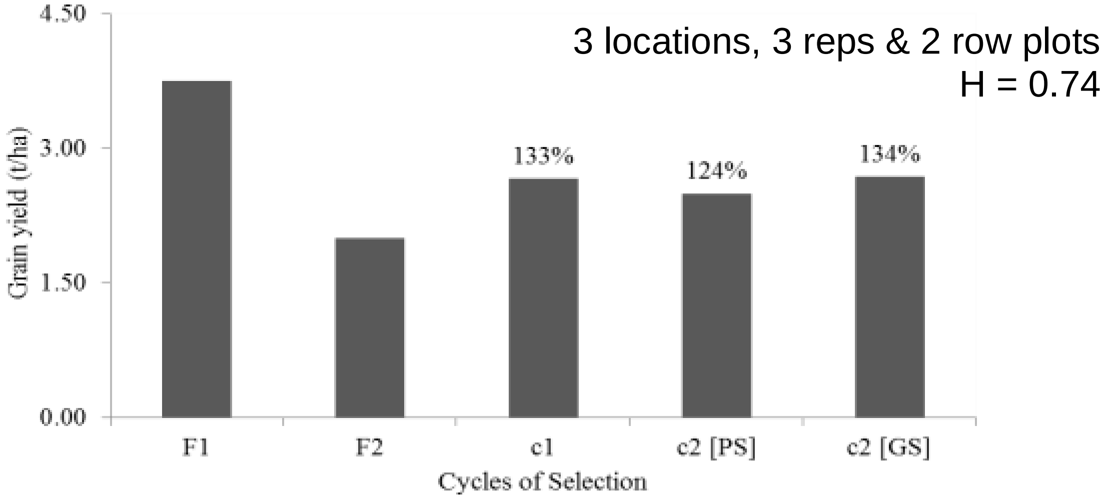


Figure 7. Selection response in using phenotypic (PS) and genomic selection (GS) in different populations

In order to make use of a range of promising sources in the breeding program and especially for combining more traits of interest, it is more cost-effective and efficient to use multi-parent synthetic (MPS) populations. The CIMMYT program developed a total of six MPS populations for combining drought- and water-logging tolerance (three each in HG-A and B) and four populations combining drought- and heat-stress resilience (two each in HG-A and B), by inter-mating the selected 8-to-10 lines within a heterotic group. The lines involved in developing these populations includes promising donor lines for respective abiotic stresses and a few elite Asia-adapted lines with proven commercial value and resistance to common diseases. However, these are susceptible to abiotic stresses. Cycle-1 was constituted by inter-mating the top 10 percent $F_{2:3}$ progenies on the basis of their test-cross performance spanning several locations under stressed and un-stressed environments. Marker, haplotype and quantitative trait loci (QTL) effects are being estimated by analysing the genotype of $F_{2:3}$ families and phenotype datasets from $F_{2:3}$ test-crosses. The populations will be subjected to three-to-four cycles of marker-only selection (RC-GS) for grain yield (GY) across stressed and un-stressed environments. These will be source-populations for deriving elite stress-resilient lines using double-haploid technology and eventually developing a new generation of stress-resilient hybrids for stress-prone targeted environments of South and Southeast Asia. Improved populations may also be used directly by farmers, as open-pollinated varieties in stress-prone environments and remote locations.

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