DOI: 10.17707/AgricultForest.62.3.20

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IMPROVEMENT OF SELECTION EFFICIENCY IN WHEAT GENOTYPES FOR VARIABLE RAINFED ENVIRONMENTS

SUMMARY

Most countries in the world depend primarily on rainfed agriculture for their grain food and there are strong reasons to believe that investments in low-yielding rainfed agriculture could have large impacts on poverty reduction. Most works in crop physiology related to breeding does focus on either yield potential or yield under stressful conditions which may reverse performance in other environments. These finding may explain why past breeding programs have largely not as expected to produce an impact on subsistence agriculture in developing countries. Correlation between the same traits in two environments may be negative or positive, depending on the environment where the experiment was grown. Crop selection in natural rainfall conditions vary in different years with additional stress-managed experiments, particularly when error variance is high and heritability estimate is low, resulted in optimum cultivar selection. These cultivar, yield better than any other available cultivar in high to low rainfall conditions, moreover an economic production under severe drought stress and therefore, increased productivity in a wide range of unpredictable rainfed environments. A researcher can use improved statistical design and analysis techniques, in multienvironments information, and consider secondary traits for making selection decisions. These alternative traits should still be much simpler than the complex genes controlling ultimately yield itself under a wide range of conditions. Earliness, canopy temperature, maintaining high kernel weight and leaf senescence are considered inherent heat and drought tolerance in wheat.

Keywords: Selection environment, Drought, Heat, Secondary traits, Alpha-lattice.

INTRODUCTION

Most of agriculture land area, around 80%, is under rainfed agriculture (FAOSTAT, 2005). The importance of rainfed agriculture varies regionally but produces most food for poor communities in developing countries. Of the 850 million undernourished people in the world, essentially all live in poor, developing countries, which predominantly are located in tropical regions (UNSTAT, 2005).

Almost, 0.70 of variation in wheat grain yield, and the reason for the

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Notes: The authors declare that they have no conflicts of interest. Authorship Form signed online.

discrepancy between actual and potential yield, was caused by water deficit during the critical period (i.e. 30 days before and 10 days after flowering; Fischer 1985) and high grain filling temperature (Calvin˜o and Sadras, 2002). Quantification and qualification of the discrepancies between actual, attainable and potential yield are important to improve productivity of farming systems.

It is important to combine expertise from different disciplines to identify and overcome crop genetic and physiologic limitations in addition to decision for experimental management to yield under unfavourable environments, particularly under heat and drought.

Recent developments include technologies that can lead to improved utilization of genetic resources, improved selection methods, improved statistical analysis, and improved targeting of production environments. They have the potential to allow for the development of new varieties more rapidly, and/or varieties with enhanced productivity in targeted environments (Bernan and Peter, 2007).

Breeding to raise both yield potential and yield further under environmental constraints through improved adaptiveness will be of paramount importance (Araus et al., 2002; Slafer et al., 2007). There is good evidence – in wheat at least – that improved genetic yield potential of cultivars have impact in both favourable as well as marginal agro-ecosystems (Calderini and Slafer 1999; Reynolds and Borlaug, 2006). Although, the spread of modern cultivars into drier areas has been much slower and their impact on yields far weaker than that in favorable climatic areas. The annual gain in genetic yield potential in drought environments is only about half (0.3-0.5%) of that obtained in irrigated, optimum conditions (Timothy et al., 2005). Ever the less, considerable improvement in the adaptation of wheat to dry areas has been made by plant breeders over the last 50 years. The adoption of modern varieties however, has lagged behind that in irrigated areas and the percentage yield advance has been considerably lower (Trethowan and Pfifer, 1999).

An FAO study (FAO, 1998) considered that it would be an error to disregard the potential to increase food production from dryland agriculture because of the difficulties associated with it; where dryland agriculture is inefficient, there is scope for increasing food production by improvement.

Plant improvement is dependent upon the screening of a wide range of germplasm for our major crops in order to identify genetic variation in major traits involved in stress resistance (Lopes and Reynolds, 2010; Richards et al., 2010; Saint Pierre et al., 2010).

The effect of selection environment on the performance of breeding material in a range of environments is a frequently debated fundamental breeding question.

Optimum environment for selection

Three strategies have been considered in relation to the optimum environment for selection (Byrne et al., 1995). Given that the optimum environment for selection is one which maximizes genetic variation, and hence response to selection in the target population of environments, the first strategy is based on the assumption that these are the characteristics of an environment where growing conditions are optimum or near-optimum. The second strategy assumes that the optimum environment(s) for selection should be as representative as possible of the target population of environments (Blum, 1988). When the breeding program serves a target population of very diverse environments, where genotype by environment interactions are expected to be large, selection should be for specific adaptation (Ceccarelli, 1996) through decentralized selection (Simmonds, 1984; Ceccarelli et al., 1996). The third strategy, the alternate use of optimum and stressed conditions has been used to select genotypes that yield well in both conditions (Calhoun et al., 1994).

Mohammadi and Fathi (2004b) reported that Selection efficiency of barley genotypes for stress conditions was estimated 1.29 in non-stress environment and 1.6 when genotypes were selected in stress conditions for favorable environment.

Identify and characterize dryland wheat regions which affected by heat and drought stress are not well defined even now, and their characterization with a high density of poor farmers will permit more precise targeting of traits to current and anticipated stress profiles.

Annual precipitation in dryland regions commonly ranges from less than half of average in a dry year to more than twice average in a wet year, which renders the use of averages of little use in planning agricultural and natural resource development. Breeding for these environments, where the frequency, timing, duration and severity of abiotic stresses, such as temperature extremes and drought, are unpredictable and variable, is considered slow and difficult (Passioura, 1986). However, A large body of recent work has demonstrated that new opportunities exist to improve the adaptation of wheat to heat and drought stressed environments (Trethowan and Mujeeb-Kazi, 2008; Rebetzke et al., 2009; Reynolds et al., 2010). The CIMMYT wheat program follows a system of breeding for drought tolerance in which yield responsiveness is combined with adaptation to drought conditions (Timothy et al., 2005). Conventional breeding with a special focus on adaptation to marginal environments provides a necessary baseline in terms of genetic backgrounds into which new traits and their genes can be introduced (CIMMYT and ICARDA, 2011).

Some genotypes are only favorable in one specific environment, like landraces which have been adapted for sever local stresses or bred cultivars which genetically modified for high yield in full irrigation conditions. The optimum variety should have superiority/acceptability in environments with different stress intensities.

A recent review of breeding progress pointed out that selection for high yield in stress-free conditions has, to a certain extent, indirectly improved yield in many water limiting conditions (Cattivelli *et al.*, 2008). But, in several crops and several environments, cultivars or breeding lines selected under optimum conditions, do not perform well under stress, which is common in low-input agricultural systems where crop production is limited by abiotic stresses (Byrne et al., 1995; Chapman et al., 1997). On the other hand, the genotypes selected for low yield conditions will probably perform better than those released for high yielding environments when grown under very poor environments. But, they have penalties in yield in wet and moderate conditions which have more frequencies in many regions. In the other words, for rainfed areas with variable frequency of drought stress, this type of genotypes with superior performance under most situations and economic production under sever drought stress with low frequency events occurance.

These genotypes developed through repeated selection cycles under high to low yielding conditions have (1) a higher probability of giving high yields under optimum to low yielding conditions, and (2) a lower probability of giving yields below an economic threshold than genotypes selected in low yielding environments. This type of germplasm has a lower maximum yield when high yielding events occur.

The relative efficiency of indirect versus direct selection can be predicted by the magnitude of the heritabilities and the genetic correlation coefficient. If A is the trait to be improved in environment X by selecting in environment Y, then (Falconer, 1989): CR/Rx = rG h_y/h_x where CRx, is the correlated response in environment X when selection is done in environment Y, Rx is the direct response when selection is done in environment X, rG is the genetic correlation coefficient between Ax and Ay, and hx and by are the square roots of heritabilities of A in the two environments.

The genetic correlation for grain yield between low- and high-yielding environments seems to decrease as stress intensity in the low-yielding experiment increases (Cooper et al., 1997). A major reason for this is the large genotype-by-environment (G×E) interactions that are usually encountered for grain yield among a range of abiotic-stressed target environments over space and times (Fukai et al., 1999).

If rG between yield measured in different environments tends to become negative as the differences between the two environments increase, then selection in one environment tends to become irrelevant to the other environment regardless of the relative magnitude of heritability. This does not preclude that occasionally individual genotypes can be found with a relatively good combination of yield in low-yielding environments and high-yielding environments because estimates of rG are averages for a population of genotypes. However, screening a large number of genotypes only under high-yielding environments implies a high probability of discarding many potentially high-yielding genotypes in low-yielding environments.

A number of studies with barley and other crops (see Ceccarelli, 1989 for a review) suggest that different alleles of the same genetic system have a positive or negative effect depending on the environmental conditions. Falconer (1989) believe that the alleles controlling high grain yield in low-yielding conditions are at least partially different from those controlling high grain yield in high-yielding conditions. Therefore, selection in high-yielding environments is expected to produce a negative response or no response in low-yielding environments. This may explain why crop varieties bred under high-yielding conditions failed to have an impact in low-yielding agricultural systems.

Screening of breeding materials for grain yield is an expensive procedure and sometimes produces inaccurate results due to the complex genetic nature of yield. The difficulty of selecting for improved adaptation particularly under abiotic stresses makes the use of indirect measures attractive to plant breeders.

Indirect selection

Struggle had been made primarily through the use of empirical breeding approaches by concentrating on yield and yield components in wheat. These traits are genetically complex and are not easy to manipulate.

Many recent works have showed that new opportunities exist to improve the adaptation of wheat to heat and drought stressed environments (Trethowan and Mujeeb-Kazi 2008; Rebetzke et al., 2009; Reynolds et al., 2010). Conventional breeding with a special focus on adaptation to marginal environments provides a necessary baseline in terms of genetic backgrounds into which new traits and their genes can be introduced. However, specific research objectives to identify and accumulate new and appropriate combinations of stress-adaptive traits must follow a systematic approach, since there is still much to learn about how potentially useful traits (and their genes) interact—with each other, with different genetic backgrounds, and across the vast range of environments in which they must be deployed.

Significant genetic progress has been made for grain yield of wheat in the low input rainfed production systems in Australia. This progress has largely resulted from direct selection for yield and broad adaptation, based on the results of multi environment trials, in combination with strategic use of indirect selection for sources of specific adaptation to characterized environmental limitations (Bänziger and Cooper., 2001).

It is possible to predict whether the use of a secondary trait can enhance expected progress in selection by calculating its genetic correlation with yield and heritability. Indirect selection for a single secondary trait results in greater progress for grain yield than direct selection for grain yield when $hGY<|rGhST|$, where hGY and hST are the square roots of the heritabilities of grain yield and the secondary trait, respectively, and rG is the genetic correlation between grain yield and the secondary trait (Falconer, 1989). These secondary traits should not be associated with poor yields in mild stress environments while breeding programs designed for stress-prone environments.

Many traits have been studied for their use in breeding programs for drought tolerance, but only a few are currently recommendable for application in practical breeding programs. For example, CIMMYT (Reynolds *et al.*, 2001), IRRI (Lafitte et al., 2003) and (Blum and Neguyen, 1997) recommend the use of flowering and maturity dates, changes in stay green (e.g., leaf death score), and low canopy temperature.

Days to heading: Earliness is one of the first attributes optimized by breeding programs (Slafer, 2003) and a major trait related to the adaptation of cultivars to particular areas. It is probably the most effective means to increase yield in regions where grains fill under severe water and heat stress (Passioura, 1996; Slafer and White Church, 2001).

Phenology is the most widely used secondary trait because of ease of measurement and relatively high heritability (e.g., Bänziger *et al.*, 2000). However, this approach has several limitations, for example, in winter grown wheat, confers on genotypes better performance (in terms of yield and stability) in severe to moderate drought environments. But, very early varieties may suffer yield penalty in good seasons. Their sensitive reproduction stages may coincide with late in-season freezing events, then, cause ear infertility and also very early flowering usually increase bird damages.

Canopy temperature: When water evaporates from the surface of a leaf, it becomes cooler canopy temperature is therefore a good indicator of a genotype's physiological fitness. Moreover, leaf cooling contributes to improvement of the photosynthetic activity of leaves and prevents premature ageing. A low value of canopy temperature is indicative of good expression of this trait under heat (Araus et al. 2002) and different drought stress conditions (Mohammadi et al., 2012b).

So many research works have demonstrated that root characteristics are important drought adaptive attributes (Manschadi et al., 2008; Reynolds et al., 2007; Christopher et al., 2008). However, root traits are difficult to measure in realistic field conditions (lopes et al., 2010) and, therefore, cooler canopy temperature has been suggested as a surrogate indicating a genotypes ability to maintain transpiration through access of roots to water deep in the soil profile (Olivares-Villegas et al., 2007, Reynolds et al., 2007).

Measurement of canopy temperature in a field plot is easily, cheaply and quickly (within a few seconds), with a simple infrared thermometer.

Thousand kernel weight: The optimum temperature range for reaching maximum wheat kernel weight is 15-18°C, higher temperatures reduce the duration of grain filling. This reduction is not compensated by the increase in rate of assimilates accumulation and in turn, accelerate maturity and significantly reduces grain weight and yield (Mohammadi, 2001, 2012). Acevedo et al. (1991) reported a 4% reduction in grain weight over a range of 17 to 24°C, for each °C increase in mean air temperature during grain-filling.

Wheat genotypes that are able to maintain high individual kernel weight despite heat stress may possess a high level of heat tolerance (Hays et al., 2007; Plaut et al., 2004; Reynolds et al., 1994; Mohammadi, 2012). There is genetic variability available for such tolerance among wheat genotypes (de Lespinay, 2004; Sharma et al., 2004b and Mohammadi, 2012a).

Leaf senescence: Delayed senescence (stay-green) is considered an important component for sustaining yield potential and in some cases also for sustaining yield under stress during grain filling (e.g. Borrell and Hammer 2000; Sanchez et al., 2002). Often, crop cultivars bred for water-limited environments by selection for yield under stress have a constitutively reduced leaf area. Pathways for constitutive reduction in plant size and leaf area are smaller leaves, reduced tillering, and early flowering. Reduced growth duration is associated with reduced leaf number (Blum, 2004). A crop plant designed for constitutive moderation of water use by the above pathways cannot attain high yield potential.

Leaf senescence is under relatively simple genetic control and can be readily improved by conventional or molecular breeding (Borrell and Hammer, 2000).

Statistical analysis

Experiments conducted under low-yielding conditions have a higher frequency of producing statistically non-significant differences (i.e., $p > 0.05$) or having a large coefficient of error variation for grain yield than experiments conducted under high-yielding conditions. This is because the error variance of grain yield usually does not decrease as much as the genetic variance when moving from high- to low-yielding conditions (Bänziger et al., 1997). Breeders often discard experiments with statistically non-significant genotype effects or large coefficients of error variation and thus do not consider that information when making selection decisions from the results of multienvironment trials. It should be emphasized that neither of these results dictates that there are no real genetic differences among the germplasm units included in the trials, but they do indicate that if the differences exist they will, in most cases, be difficult to detect with a satisfactory level of confidence.

When analyses of yield were conducted within states or regions, the three factor genotype-by-site-by-year interaction was generally found to be the largest component of variance. Within this region, the genotype-by-site interactions are usually the smallest interaction component. Since the three-factor genotype by-site-by-year interaction is usually found to be the largest source of G×E interaction for yield, it is not sufficient to concentrate on only the spatial or temporal aspects of environmental variation in the target population of environments but rather on the interplay of these spatial and temporal dimensions of environmental variation and the influence of this interplay on the yield performance of genotype (Mohammadi, 2011a, Mohammadi et al., 2012a and Mohammadi et al., 2013).

Use of an alpha-lattice design in replicated yield trials of bread wheat at Gachsaran Dryland Agricultural Research Station in 2010-11 under sever heat drought and stress resulted in an average efficiency 15% higher than the randomized complete block design when average variance was used as the comparison criterion. The results of this study show that alpha lattice design provided smaller standard errors of differences, coefficients of variation and error mean squares as compared to RCBD providing efficiency in comparing different entries/lines. Alpha-lattice was generally most efficient when the C.V.s of the trials were high. It was also slightly more efficient for low-yielding than for high-yielding trials, and for rainfed than for irrigated trials. Since the changeover to alpha-lattice designs requires no new major input or changes in present field layout (Yau, 1997).

Alpha lattice has been shown can be more efficient than RCBD in field trials conducted in the UK (Paterson and Hunter, 1983), Yau (1997) in ICARDA and Mc Laren in IRRI. It appears to have the potential to replace RCBD in many trials.

Modern alpha lattice design doesn't suffer from the number of entries and block size. Thus, it has much flexibility field layout. Moreover, It doesn't need definite layout before planting and it is possible to analyze the data of an experiment by alpha lattice design, while, it was planted based on RCBD layout.

YAU, (1997) reported the use of alpha lattice design in international yield trials of different crops and found average efficiency 18 % higher than the RCBD. Alpha lattice is more effective with larger trials than with those involving small numbers of entries.

Managed- stressed experiments

Traditionally, crop improvement and natural resource management were seen as distinct but complementary disciplines. Improved varieties and improved resource management are two sides of the same coin. Most farming problems require integrated solutions, with genetic, management related and socio-economic components.

In developing countries, farmers have traditionally grown landrace cultivars, which are well adapted to serious moisture stress conditions. However, these traditional cultivars are generally poor yielding in "good years" when rainfall is more plentiful. Some researchers believe modern cultivars have consistently outyielded older cultivars, even in the lowest yielding conditions of each particular study (Slafer and Andrade, 1993; Calderini et al., 1995). Based on our experiences, some new improved cultivars such as Zagros and Koohdasht which were released for semitropical dryland regions of Iran, yield the same as or even more than local/landraces cultivars in dry years (with more than 0.7 t/ha in farmers conditions), yet will respond to more favorable moisture and nutrient conditions.

Under a particular pressure of environmental stress, cultivars with high yield potential produce less than certain cultivars that have lower yield potential but seem to be better adapted to stress. For most cereals grown under water-limited conditions the crossover occurs at a yield level of around 2–3 t/ha (e.g. Blum and Pnuel, 1990; Ceccarelli & Grando 1991), which is approximately one-third of the yield potential. The main reason for a crossover under conditions of variable water supply is an inherent difference among the tested cultivars in drought resistance, beyond difference in their yield potential (Blum, 2005). It seems this border depends on characterization of considered target environments.

Crop selection performed in nurseries with normal natural growing conditions is translated to cultivars with increased productivity in a wide range of growing conditions, from mild (approx. 4-6 t/ha) to moderate stress (approx. 2-4 t/ha) and even more stress (approx. 1-2 t/ha) environments with low probability frequency. However, in selection environments subject to sever drought stress in most years, the situation may change.

When programs selection for yield was performed under low-yielding stress conditions, large differences were seen among different years, locations, and studies in the heritability estimates for yield under stress in a given crop.

Heritability for yield under stress largely depends on 2 key factors: (*a*) the existence of genes for drought resistance in the population, which are effective in the stress environments under which selection is performed (Blum et al., 2001), and (*b*) the degree of control over the homogeneity and general stress conditions in the selection nursery (Blum 2005). Because of the difficulty of choosing a few representative selection environments for a target population of environments where low yields may be caused by a number of interacting and varying abiotic stress factors, CIMMYT approached breeding for low input conditions by simulating abiotic stress factors that are important in the target environment and exposing breeding experiments to a clearly defined abiotic stress factor. These selection environments were termed ‘managed stress environments’(Bänziger and Cooper 2001).

The use of managed stress environments permitted controlled and quantifiable consideration of the factors that affect breeding progress. Because these trials were established under researcher-managed conditions and thus exploitation of a much larger genetic variance and higher selection intensity than it is usually possible at the advanced breeding stage. Error variance was kept low and heritability was kept high by using a combination of improved statistical design and analysis techniques, choosing fields with rather uniform soil texture and depth, maintaining optimal plant stands, and using well-bordered trials (Bänziger et al., 1995; Lafitte et al., 1997).

Control over the homogeneity and general stress conditions in the selection nursery like weeds, diseases, pests, inherent soil variability, etc. is effective in the stress environments under which selection is performed (Blum et al., 2001). Selection in stress-managed environments does not suffer from these additional problems under stress than in unmanaged environments. Microelement deficiency or parasitic nematodes, whose effects on productivity are severely exacerbated under moisture deficit, confounding potential genetic gains associated with drought adaptation *per se* (Reynolds and Trethowan 2007).Therefore, with the appropriate genetic materials and minimisation of the error variance, heritability for yield under stress can be high and selection effective, particularly, in sever drought stress.

However, as the genetic variance for grain yield is smaller under low input conditions, selection progress is less and breeders may be disappointed when regrowing germplasm selected for improved productivity in the following year, even more so if that year exposes the germplasm to different environmental constraints.

These managed environments may be conducted on research stations or on-farm. In a number of cases this has progressed to the point where these managed environments have been included as additional environments in multienvironments.

Germplasm developed using combined results from managed stress and normal natural environments indeed proved to have a higher yield level and stability, than evaluation across a random sample of trials from the target environments that may include sever drought environments with low heritability accompanied high error variance. It was observed that genotype-by-stress interactions for the particular targeted abiotic stress factor were at their highest, if stress levels were severe, when stress is uniformly severe which is rare in the field. wheat cultivars tested in a particular set of stressful conditions may not show the same performance in another set (Cooper et al., 1997).

Many scientists have chosen a midway and believe in selection under both stress and non-stress conditions (Fischer and Maurer, 1978; Clarke et al., 1992; Fernandez, 1992). Selection for high yield in an optimum environment is effective because genetic variation is usually maximized and genotype-by-environment interactions are low (Richards, 1996). However, genotypes selected in optimum environments may not yield well in drought stress environments (Mohammadi et al., 2011b). On the other hand, selection under drought stress conditions is often complicated by low heritability of traits, non-uniform testing conditions and large genotype-by-environment interaction.

Several indices have been utilized to evaluate genotypes for drought tolerance based on grain yield in different environments. Rosielle and Hamblin (1981) defined stress tolerance (TOL) as the differences in yield between the stress (Ys) and non-stress (Yp) environments and mean productivity (MP) as the average yield of Ys and Yp. Fischer and Maurer (1978) proposed a stress susceptibility index (SSI) for cultivars. Fernandez (1992) defined an advanced index (STI= stress tolerance index), which can be used to identify genotypes that produce high yield under both stress and non-stress conditions. The other yield based estimate for drought resistance is geometric mean productivity (GMP). The geometric mean is often used by breeders interested in relative performance, since drought stress can vary in severity in field environments over years (Ramirez & Kelly, 1998). The optimal selection criterion should distinguish genotypes that express uniform superiority in both stressed and non-stressed environments from the genotypes that are favorable only in one environment.

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