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Multi Environments and Genetic-Environmental Interaction (GxE) in Plant Breeding and its Challenges: A Review Article

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Abstract: *Plants are sessile creatures which have to survive with environmental fluctuations to guarantee species reproduction for perseverance in nature. Genotype by environment interaction is the differential reactions of genotypes over wide environments. Sustaining high agricultural production; the development of varieties with high yield potential is the vital objective of plant breeders in crop advancement. In addition to high yield potential, a new cultivar has to have stable performance and wide adaptation over environments. The presence of genotype by environment (GxE) interaction is a major concern to plant breeders, since large interactions can reduce advantages from selection and complicates identification of superior cultivars and is of major importance for crop breeders, given that phenotypic response to change in environment is different among genotypes. It is important in the development and evaluation of plant varieties because they diminish the genotypic stability values under different environments. So, a key of focus areas in the future plant breeding should be GxE specially, in developing country for adequate varieties for climate change pressures and abiotic and biotic factors by advancing human skill.*

Keywords: *Genotype, Environment, Interaction, Plant breeding*

1. INTRODUCTION

Genotype by environment interaction denotes to the differential reactions of genotypes over sites (Bavandpori *et al*., 2015). Genotype by environment interactions (GXE) is a key factor to be studied in plant breeding. The repeatable GxE interactions resulted, change the ranking of genotypes across environments, and are meaningful for the specific breeding strategy (Sabaghnia *et al*., 2008). It is a common for most quantitative traits such as yield, plant height, weight etc., of economic importance.

Genotype x environment (GxE) interaction and yield-stability analysis has continued to be important in measuring varietal stability and suitability for cultivation across seasons and ecological zones. The analyses of genotype x environment has focused on the identification of stable genotypes for cultivation.

According to (cooper 2001) the extent of genotype by environmental interaction is higher where there is a wide-ranging variation between environments in incidence of the same stress such as, climate, soil, biotic and management factors. Environmental factors can be micro- or macro-, non-organic or organic, and internal or external. Plant growth and yield are affected by both intercellular and external environments. Intercellular environments in plants are largely dominated by what are essentially enclosed in vacuoles, which consist of water (inorganic and organic molecules), waste products and small molecules with internal hydrostatic pressure or turgor, temperature, and an acidic pH maintained.

The interior environments are mostly affected due to the fluctuations of pH, osmotic pressure and temperature, etc., caused by material exchange and signal transduction with external environments. Through a series of receptors, signal transductions and responses, plants make full responses to specific external environmental factors, resulting in ion trans membrane transport, metabolic pathway regulation, cytoskeleton modification and gene expression regulation (Nicotra *et al*. 2010, Yunbi Xu, 2016). Plant breeding categorizes reasons of genotype by environment towards predictability, detached predictable from unpredictable, separate G and E components of the GxE Structured models.

Hence, understanding the genetic mechanism driving GxE in plants is an essential step for being able to forecast yield performance of crop cultivars, to adapt breeding strategies according to the targeted locations (El-Soda *et al*., 2014). So, the objective of this paper is to review multi environment and genetic-environmental interaction (GxE) in plant breeding and it challenges.

2. LITERATURE REVIEW

2.1 Historical Back Ground on Genotype-by-Environment (GxE)

2.1.1 Study of GxE During the Early 20th Century

The biometrical genetics conceptualization of GxE was popularized by Ronald Fisher from plant and animal studies for the purposes of optimizing crop yield Tabrey (2008). This perspective focused on the amount of genetic and environmental differences responsible for variation in populations. A biometrical genetics definition of GxE refers to a genotype-specific sensitivity to environmental exposure of an organism Fisher & Tedin (1932). Fisher used ANOVA to test data generated from carefully planned plant and animal experiments and expected to detect GxE on a statistical level when, at the functional level, genetic differences were observed as sensitivity to the environment. Interestingly, Fisher was not convinced that GxE was an important influence on traits and treated it as a nuisance because he found that he could often remove significant GxE through a simple transformation of the scale of the environment.

2.1.2 Limitations of the Biometrical Genetics Definition of GxE

Lancelot Hogben, a contemporary of Ronald Fisher, studied the role of GxE on individual development across changing environmental conditions. This focus on the role of the genetic and environment influences on development highlighted fundamental differences regarding the goals of GxE research for the two scholars. Fisher focused on the difference between the detection and estimation of the magnitude of GxE as a source of variation while Hogben concentrated on the characterization of GxE as a biological mechanism in development.

These differences and the ensuing debate highlighted certain assumptions and limitations of the biometrical genetics approach to GxE that made application to human populations a challenge. Initially, GxE research may not have addressed the nature of genetic and environmental influences to appropriately reflect processes related to human outcomes. For example, initial studies of GxE using breeding experiments generally assumed genetic and environmental influences to function independently of one another. In humans, it is likely that the genotype of an individual could be correlated with exposure to a particular environment (genotype-environment correlation). Second, initial studies of GxE focused on cross-sectional experiments which did not take into account the role of development across time or of non-linear interactions. Third, the original approach to analysis of GxE evaluated genetics using different breeding lines selected for specific characteristics.

Therefore, characterization of GxE via classic biometrical approaches reflects variation due to overall additive genetic influences. It is possible that there may be disconnect between characterizations of GxE via classical biometrical genetic approaches and those testing the influence of specific genes using modern genotyping technologies. Fourth, classical biometrical studies often focused on single, specific environmental exposures. The ability to interpret GxE results to multiple levels of environmental exposures (i.e. family vs. neighborhood) was limited and beyond the focus of early GxE studies. Fifth, genetic and environmental contributions in breeding experiments were assumed to have and many times were measured as continuous distributions. However, the measurement of human behavior is more difficult to accomplish compared to breeding experiments. Therefore, it is possible this assumption may not be appropriate for current measures of human behaviors.

2.1.3 The Study of GxE during the mid to late 20th Century

Focus on Human Studies of GxE, some of the limitations of classical biometrical genetics approaches to GxE research has been addressed in recent decades. For example, studies of human behavior have spent an enormous effort on the issue that genetic and environmental influences are not independent of one another. Further, the detection of statistically significant GxE may be due to either gene-environment correlation (rGE), GxE or their combination.

The work of Cattell (1960) and Loehlin (1965) detailed some of the first approaches to detecting and estimating both GxE and rGE simultaneously in humans. Jinks and Fulker (1970) later adapted these approaches to fit within the biometrical genetics framework using data from monozygotic and dizygotic twins. Plomin, DeFries and Loehlin (1977) were the first to detail the concept of rGE and summarized study designs and statistical approaches for detection (1977). Scarr and McCartney (1983) extended the concept of rGE to a developmental model in order address the role of rGE in human behavior across the lifespan.

Prior breeding studies were unable to test for the effects of specific genetic influences. Additionally, these studies generally did not address the complexity of multiple environmental influences working together as they do for human outcomes. Nevertheless, studies in the biometrical genetics tradition provided some expectations regarding the nature of gene-environment interplay. Further, they emphasized the need to study many genetic and environmental influences on a trait to understand the mechanisms underlying a trait. These studies identified three specific characteristics on the nature of GxE.

The statistical perspective on GxE focuses on the detection of statistical interactions in general and GxE specifically, which strictly refers to modeling the effect of GxE as the product of two variables each with their own main effects. The presence of GxE is first identified as a statistically significant interaction effect, which may be detected through appropriate study design and statistical tests typically as a departure from only additive main effects.

The biological perspective focuses on the conceptual framing of GxE as a biological process. This refers to the interaction between elements in a biological system or across various systems to propagate a mechanism. Typically, GxE as a biological interaction attempts to understand the question of how genetic and environmental influence function together. The presence of biological GxE does not necessarily have to involve statistical interaction and as such genetic and environmental influences may only be detected as significant additive main effects

2.2 GxE and its Challenges

GxE and yield stability have been encounter to the breeders and biometricians for a long of time because it complicates the selection of superior genotypes by reducing the genetic progress. A GxE is important to minimize the usefulness of the genotype means across locations or environments for selecting and advancing superior genotypes to the next stage of selection (Pham and Kang, 1988, Natalia de Leon *et al.*, 2016). Plant breeders have managed these interactions throughout the history of crop domestication, crop improvement, and dispersal, and within recent history through the formalized procedures of plant breeding.

Environmental effect is the greatest, but is irrelevant to selection. In Ethiopia, the relationship between selection environments and target production environment had been a fundamental problem because many of the selected activities performed by the conventional approach are in on-stations which are good production environments (Ceccarelli, S. and S. Grando, 2007, Melkamu Temesgen *et a.l*, 2015). Many statistical approaches consider all of the phenotypic variation (i.e., means across environments), which may be misleading. GXE Interaction is not merely a problem, it is also an opportunity" (Simmonds, 1991). The varietal stability could be challenged not only due to the change in the test environment but also due to change in growing season per environment (Dagnachew *et al.*, 2014). Some environmental variations are predictable (soil type, soil fertility, plant density) and others also may be unpredictable (rainfall, temperature, humidity etc.).

2.3 Importance of Studying GxE

Genotype x environment (GXE) interactions is important in the development and evaluation of plant varieties because they reduce the genotypic-stability values under diverse environments (Hebert *et al.*, 1995). Significant achievement in crop production may be possible by breeding varieties for their stability for yield and yield components (Singh et al., 2009; Lal *et al.*, 2010). Statistically, G x E interactions are detected as a significantly different pattern of responses among the genotype across environments and biologically, this will occur when the contributions (or level of expression) of the genes regulating the trait differ among environments (Basford and Cooper, 1998).

A conceptual GXE interaction is commonly depicted as the slope of the line when genotype performance is plotted against an environmental gradient. Non-parallel, but non-intersecting lines indicate that the rank of cultivar performance stays the same across environments. Lines that intersect indicate that there is a change in rank of cultivars across environments, and the optimum cultivar will be location specific. GXE affects virtually every aspect of the decision making process involved in plant breeding programs including identification of the most relevant testing environments, allocation of resources within a breeding program, and choice of germplasm and breeding strategy (Natalia de Leon *et al*., 2016).

GXE also used as a measurement of the plasticity of genotypes in terms of the expression of specific phenotypes in the difference (variable) environmental influence. The scientific field concerned with phenotypic plasticity, team researchers across disciplines: the ability of genotypes to express different phenotypes when influenced by different environment (Phenotypic plasticity is the ability of an organism to express different phenotypes depending on the biotic or abiotic environment). The divide comes from the focus that different groups of researchers have taken to study this phenomenon.

Crop performance depends on the genotype, environment and the interaction between genotype and environment (Mehdi Mohebodin *et al*., 2016). To test broadly adapted and stable genotypes, information dealing with adaptation of variety and stability over environments (locations and years) is important. Identification of stable genotypes which show the least G×E interaction is important consideration in sites where environmental fluctuations are noticeable. G×E interaction occurs when the performance of the genotypes is not consistent from one environment to another that complicates the selection and/or recommendation of genotypes.

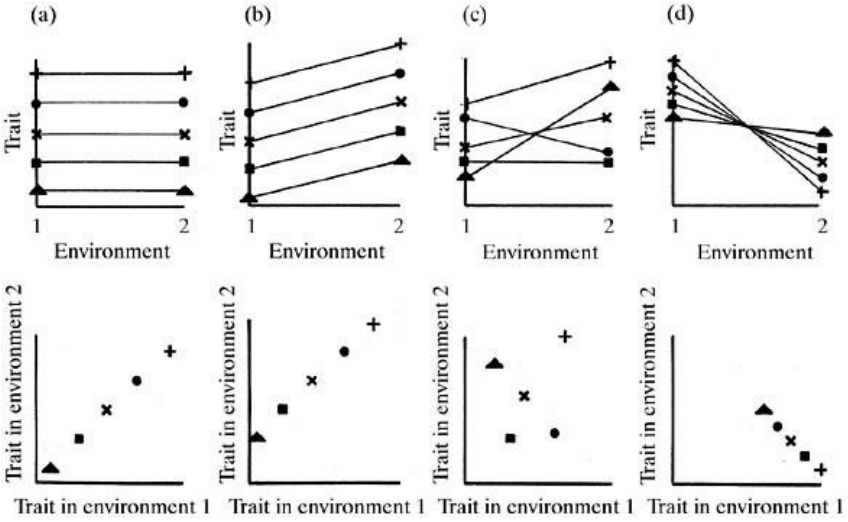

Figure1. *Reaction norms for five genotypes (top row). Each line connects the value of a genotype's life-history trait in one environment to its value in the other; genotype values might be estimated, for example, by half-sib family means. Four possibilities are considered (a-d). The corresponding between-environment correlations are shown in the bottom row. Genotypes in (a) and (b) can be considered to be generalists, whereas those in (d) are specialists; (c) represents an intermediate case. Source: Guntrip & Sibly, 1997*

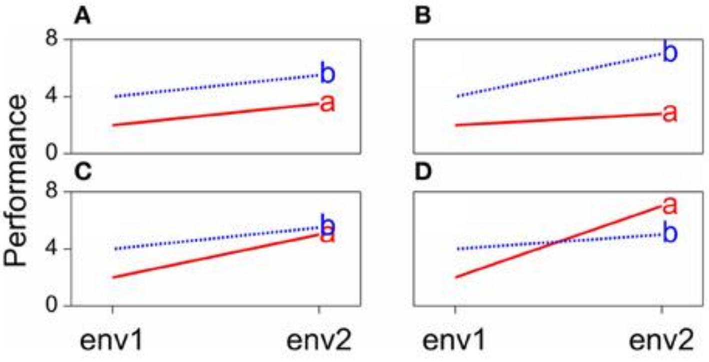

Figure2. *Genotype-by-environment interaction in terms of changing mean performances across environments: (A) additive model, (B) divergence, (C) convergence, (D) cross-over interaction. Source: Marcos et al. (2013).*

Climatic conditions were the source of oil content variation component. The stability of tested genotypes can be evaluated according to biplot for oil content. Interspecific Brassica cross derived lines interacted differently with climate conditions in the observed environments (Jan *et al*., 2018).

The quality traits of wheat interact with the environment, so it is important to evaluate and quantify to what degree factors like the environment (E) and genotype x environment interaction (GEI) are responsible for phenotypic variation in the traits. The effect of E on certain quality parameters varies, but it is generally stronger on protein content (PC) and protein related parameters (Fowler *et al.*, 2016).

From the breeding point of view, it is important to understand the masking effect of environment relative to actual heritable traits by determining the GEI and identify a trait which shows stable effect across different environment (Lin *et al.*, 1988). Moreover, it is important to see whether the breeding programs are successful by evaluating their genetic gains. Such evaluation can help in identifying the traits that contribute to yield improvement and developing the future breeding strategies. (Cox *et al.*, 1994). For this purpose, breeding programs in many countries select historical set of cultivars and study them in different environment to determine the genetic gains achieved through breeding and selection over particular breeding period.

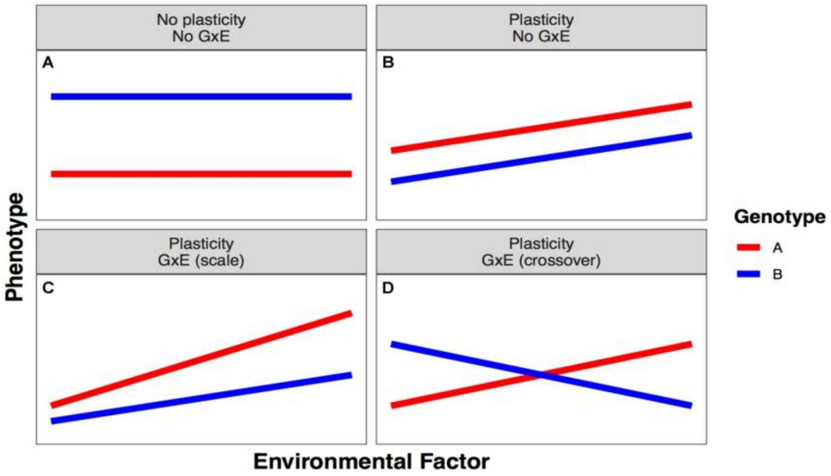

Figure3. *Example forms of linear plastic responses. (A) Neither genotype expresses different phenotypes in different environments. (B) Both genotypes exhibit the same plastic response, so there is no genotype–environment interaction (GxE). (C) Both genotypes exhibit different plastic responses that lead to a greater advantage of genotype A over genotype B as the environmental factor increases (scale GxE). (D) Both genotypes exhibit different plastic responses that cause the best genotype to change in different environments (crossover GxE).*

2.4 Types of Variation in GxE and components

2.4.1 Genotypic Variation

In plant breeding, the rate of genetic gain relies on the genetic diversity for a given trait in the breeding population (Hallauer and Miranda, 1981, Kai Luo *et al.*, 2016). The magnitude of genetic variation for plants programs will enhance the development of appropriate breeding strategies to achieve maximum genetic gain (Moll and Stuber, 1974, Kai Luo *et al.*, 2016). For example, Jahufer and Casler (2015), Kai Luo *et al*., (2016) evaluated the relative advantage in genetic gain using single trait selection, correlated response to selection and index selection, based on estimated genetic variation for a range of morphological and quality traits in switch grass (Panicum virgatum L.). Genetic variation for key traits have been reported for some of the important forage grasses and legumes: ryegrass (Breese and Hayward, 1972, Kai Luo *et al*., 2016), tall fescue (Piano *et al*., 2007), white clover (Jahufer *et al*., 2002, Kai Luo *et al*, 2016), alfalfa (Riday and Brummer, 2007).

There are three components of genetic variation: 1. Additive genetic (genes which are 100% transmitted from parent to offspring), 2. Dominant gene action and 3. Epistatic gene components (when one gene masks the effect of another gene). These three components are used for variety development. $V_P = V_{G} + V_{E} = V_D + V_{H} + VI + V_{E}$, where $V_{P} =$ Total phenotypic variance, $V_{G} =$ Genotypic variance, $V_{D} =$ Additive gene, $V_{H} =$ Dominance gene and $V_{I} =$ Epistatic, $V_{I} =$ i, j and l.

2.4.2 Phenotypic Variation

Screening of genotypes for various yield contributing traits, in all the environments and seasons following standard evaluation system (IRRI, 2013, Divya Balakrishnan *et al*.,2016). The observations on yield and morpho-agronomic traits were recorded from the field experiments.

The plant phenotype (P) is not only determined by the plant genetic composition (G) and environmental factors (E), but also their interaction (GXE), usually described by the linear model P = G + E + GXE (Visscher, P.M. *et al*., 2008, Bernardo, R., 2008, Mohamed El-Soda *et al*., 2014). Therefore, variety trials in a breeding program are usually conducted in several environments, to minimize the risk of discarding genotypes that potentially perform well in some, but not in all, environments (Kang, M.S.1997, Ceccarelli, S. *et al*.,1994, Mohamed El-Soda *et al*., 2014). In general, to predict the genotypic response to selection across environments, the narrow sense heritability (Visscher, P.M. *et al*., 2008, Holland, J.B. *et al*., 2003, Eichler, E.E. *et al*.,2010, Mohamed El-Soda *et al*., 2014) of a trait is estimated based on main effects, leaving GXE effects within the unexplained phenotypic variance, and so leading to so-called ‘missing’ heritability. In other words, missing heritability results from all sources, which can lead to departures from the simple additive effect model, including epistasis, epigenetic variants, rare variants (e.g., encountered in association mapping studies), small undetected QTL, and also GXE (Eichler, E.E. *et al*.,2010, Manolio, T.A. *et al*., 2009, cited by Mohamed El-Soda *et al*., 2014).

Evaluating genotypes in multiple environments is essential to gain insight into the extent of GXE (Bergelson, J. and Roux, F., 2010, Van Eeuwijk, F.A. *et al*., 2010, Mohamed El-Soda *et al*., 2014) and this is of great interest for crop breeders to assess how much of the selection progress achieved in one environment can be carried over to other environments (Van Kleunen, M. and Fischer, M., 2005, Nicotra, A.B. *et al*., 2010, Kang, M.S.,1997, Mohamed El-Soda *et al*., 2014).

2.5 Stability and Adaptability

Stability states to the adaptation or fitness of varieties to various groups of sites and it has been used to select stable genotypes unaffected by environmental changes while adaptability is the well survival of a genotype across any particular environment (MOORTHY *et al*., 2012, Chandrakanth N *et al*., 2016). The knowledge of stability is important for the selection of crop varieties as well as for breeding programs. Yield stability is an interesting feature of today’s plant breeding programs, owing to the high annual variation in mean yield, especially in the arid and semi - arid areas (Mohammadi *et al*., 2012). A variety or genotype is considered to be more adaptive or stable if it has a high mean yield but a low degree of fluctuation in yielding ability when grown over diverse environments.

The concept of stability has been estimated in biometrical methods including univariate and multivariate ones that have been developed to assess stability (LIN *et al*., 1986;CROSSA,1990, Chandrakanth N *et al*., 2016).The most widely used one is the regression method, based on regressing the mean value of each genotype on the environmental index or marginal means of environments (MOORTHY *et al*.,2012, Chandrakanth N et al., 2016). A good method to measure stability was previously proposed by FINLAY and WILKINSON(1963) and was later improved by EBERHART and RUSSELL (1966, Chandrakanth N *et al*., 2016). MOORTHY *et al* .(2012) successfully applied the method proposed by EBERHART and RUSSELL (1966) to calculate stability index in 46 silkworm breeds in 3 environments. This method was also applied in many crops (AKCURA *et al* ., 2005; DEWDAR , 2013, Chandrakanth N *et al*., 2016).

2.6 Methods of Measuring GXE

Plant breeders have recognized the negative implications of GXE Interaction in collection, selection, variety development and focused on developing breeding tools and resources to reduce its negative effect and taking positive advantage Interaction (Freeman, 1973; Cooper, 1999; Cooper *et al*., 2014; Sadras and Richards, 2014, Natalia de Leon *et al*., 2016). Commonly, cultivars are identified for deployment to specific environment (Cooper *et al*., 1997; Chapman *et al*., 1997, Natalia de Leon *et al*., 2016).

G x E used to manage stress trials to emphasize the effect of particular sources of abiotic stress on the performance different genotypes and for understanding the effect of particular environmental disruption on phenotypes. Most of the evaluations of the effect of the environment on performance have relied on multi-environmental field testing that represent target production environments to identify and develop cultivars (Comstock, 1977, Natalia de Leon *et al*., 2016).

These multi-location studies provide two-way tables of means for different genotypes across different environments.

Data from such two-way tables can be initially analyzed using models that incorporate the effect of the genotype, the environment, and also that partition the remaining variation into the effect of the interaction between environments and genotypes and the residual experimental error (pooled error). This provides indication of the proportion of the variance that refers to the main effect of genotype compared to GXE, but it is limited in terms of providing insight into the nature of the interaction. Much of that descriptive information, in the context of plant breeding, has been founded on the work by Finlay and Wilkinson (1963), Natalia de Leon *et al*.,(2016) and modified by others (Eberhart and Russell, 1966) which qualified GXE based on the slope of the regression of the performance of particular genotypes across an environmental gradient. The most basic models determine this quality gradient based on the average performance of all genotypes in that environment.

This methodology permits to interpolate the performance of the specific genotypes being investigated across untested environments, as long as the environments are within the range of the gradient in tested locations. This traditional concept of stability is useful for the study of phenotypic plasticity as it provides a single measurement of the slope of the regression line of genotypes along environmental gradients which can be used as the entry phenotype for genotypic-phenotypic associations, for example, to understand the genetic architecture of plasticity itself.

Other complementary and well recognized methods developed to assess environmental stability include mean-CV analysis from Francis and Kannenberg (1978) and Shukla's (1972), Natalia de Leon *et al*., (2016) stability variance.

The additive main effects and multiplicative interaction (AMMI) model was one of the initial implementations of this strategy (Gollob, 1968; Gauch, 1988, Natalia de Leon *et al*., 2016). In this context, GXE is modeled as the product of the effect of the specific sensitivity of a genotype to a latent (unobservable) environmental variable. A principal components strategy maximizes the variation explained by the products of the resulting genotype sensitivities by environmental variables (Gabriel, 1978, Natalia de Leon *et al*., 2016).

Another variant to this overall strategy came through the development of modeling strategies that incorporated not only the GXE variation but also the combined effect of the genotypic main effect and the GXE as a sum of the multiplicative terms. This general set of methods are called "genotype main effects and GXE" or GGE model (Yan *et al*., 2000, Natalia de Leon *et al*., 2016).

These multiplicative strategies are particularly useful because they provide meaningful graphical displays of performance which allows direct interpretation of the relationship between specific environments and between particular genotypes, and, in the case of GGE, direct interpretation of the effect of specific genotypes in particular environments.

From the standpoint of improving the interpretation of the effect of particular environmental effects on performance, advancement came from the incorporation of explicit quantification of environmental components to statistical models as explanatory variables. These so-called factorial regression models connect the differential sensitivity of genotypes to observed environmental variables (e.g., rainfall in May) which could be chosen based on what is needed for crop growth (van Eeuwijk *et al*., 1996). Since overall performance is what breeders are interested in, this type of analysis facilitates direct biological interpretation of performance and therefore has direct utility for practical breeding programs.

Several mixed model applications have also been proposed to analyze and interpret GXE primarily for multi-environment analysis that involves a large number of genotypes (Smith *et al*., 2005). In this context, genotypes can be modeled as random effects and their potential heterogeneity of variances (and co-variances) can be interpreted as an indication of differential genotypic sensitivity to certain environmental cues.

3. SUMMARY AND CONCLUSION

To maintain high agricultural productivity, the development of varieties with high yield potential is the ultimate goal of plant breeders in a crop improvement program. In addition to high yield potential, a new cultivar should have stable performance and broad adaptation over a wide range of environments. The presence of genotype by environment (GxE) interaction is a major concern to plant breeders, since large interactions can reduce gains from selection and complicates identification of superior cultivars and is of major importance for crop breeders, given that phenotypic response to change in environment is different among genotypes.

However, Phenotypic response is not always the same in different location as it is affected by biotic and abiotic factors environmental factors. GXE Interaction is very important to reduce the genotype means across different environments. It is continues task of plant breeders because of the environmental fluctuation across different location and through years and it is used as a measurement of plasticity of genotypes to the expression of specific phenotypes in different environments. The main purpose of multi-environment trials is to observe stability of genotypes across the environments, the identification of superior genotypes and of the location that best represents the target environment for production.

The major areas of focus in the future plant breeding include should be GxE in plant breeding pursues continually moving targets in developing country, adequate varieties for climate change pressures and many other stresses (tolerance/resistance to major abiotic stresses such as drought, salinity etc., and biotic factors such as diseases and pests) and by advancing human skill.

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