



Research Article

Genotype-Environment Interaction and Stability Analysis

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ABSTRACT

Genotype-by-environment interaction is an important phenomenon in plant breeding for developing superior genotypes for respective environment. The presence of genotype \times environment interaction in plant breeding is expressed either as inconsistent responses of some genotypes relative to others due to genotypic rank change or as changes in the absolute differences between genotypes without rank change. The success of a plant breeding program depends on its ability to provide farmers with genotypes with guaranteed superior performance in terms of yield and quality across a range of environmental conditions. Expression of a phenotype is a function of the genotype, the environment, and the differential sensitivity of certain genotypes to different environments which is known as genotype by environment interaction. Genotype by environment interaction refers to a statistical decomposition of variance and provides a measure of the relative performance of genotypes grown in different environments. Genotype-by-environment interaction can also be conceptualized as a measurement of the relative plasticity of genotypes in terms of the expression of specific phenotypes in the context of variable environmental influences. The environmental factors affecting crop yields can be classified into abiotic and biotic constraints. Actually, these factors are more intensified with global warming which leads to climate change. Abiotic stresses adversely affect growth, productivity and trigger a series of morphological, physiological, biochemical and molecular changes in plants. The abiotic constraints include soil properties (soil components, pH, physicochemical and biological properties), and climatic stresses (drought, cold, flood, heat stress). On the other hand, biotic factors include beneficial organisms (pollinators, decomposers and natural enemies), pests (arthropods, pathogens, weeds, vertebrate pests) and anthropogenic evolution. The final state of a trait is the cumulative result of a number of causal interactions between the genetic make-up of the plant (the genotype) and the conditions in which that plant developed (the environment). Plants differ in the efficiency and adequacy with which they capture and convert environmental inputs and stimuli into the biomass and organs that constitute a final product. The capture and conversion abilities of a plant are determined by its particular ensemble of genes.

Key words: Phenotype, Genotype, Genotype - environmental interaction, Stability, Biotic stress, Abiotic stress

INTRODUCTION

Genotype by environment interaction (G \times E) refers to the differential responses of genotypes across environments (Bavandpori, *et al.*, 2015). A genotype - environment interaction is a change in the relative performance of a character of two or more genotypes measured into two or more environments. In genotype-environment interaction, the magnitude of the observed genetic variation changes from one environment to another and tends to be larger in better environments than poor environments. Genotype-environment interaction is a fundamental component in understanding complex trait variation and the most challenging factor in identification of genetic variation. Interaction involves a change in rank order for genotypes between environments and the relative magnitude of

genetic, environmental and phenotypic variance between environments. The effect of genotype-environment interaction can be reduced by identifying stable genotypes across environments (Eberhart and Russell 1966). The phenotype of an individual depends upon both the genetic make-up and environmental influences. Genotype - environment interaction is considered as an important source of discrepancy in any crop and different methods have been used to distinguish genotypes for their behavior in different environmental conditions.

The term genotype refers to the genetic makeup of an organism while environment refers to biophysical factors that have an effect on the growth and development of a genotype (Basford and Cooper 1998). The basic cause of differences among genotypes in relation to production stabilities is known as the genotype \times environment

interaction. Hence, the performance of the genotypes depends on the specific environmental conditions where they are grown. The different agro-climatic regions differ with respect to climatic (temperature gradient, photoperiod and rainfall distribution) and edaphic (soil fertility and type) factors and management practices. Phenotype is the product of genotype and environment. In the presence of genotype - environment interaction, the phenotype will be the product of genotype, environment and genotype - environment interaction. Same genotype can produce different phenotypes in different environments and different genotypes can produce same phenotype in a particular environment. A stable genotype is one which interacts less with the environment and shows a minimum of genotype x environment interaction.

When the genotype x environment interaction is significant, further investigation and other specific types of interactions such as genotype x location, genotype x specific treatment such as fertility level, irrigation schedule, sowing date, genotype x season (year) and genotype x location x year should be done. In case of stability, a variety shows minimum or low variety x season (year) interaction. In case of higher adaptability, genotype x location x year interaction is low and the environments consist of predictable as well as unpredictable factors. A significant genotype by environment interaction is used to diminish the genotype means across environments for choosing and advancing high yielder genotypes to the next stage of selection. A non-significant genotype by environment interaction simplified the selection because the best genotype in one environment would also be the best genotype for all target environments. The phenotype of an individual is determined by the effects of its genotypes, the environment, and the interaction between the genotype of the individual and the environment. The genotype by environment interaction results in non-stable performances between the genotypes across environments. Genotype x environment interaction is one of the main challenges in the selection of wide adaptation in most breeding programs.

The variation in phenotype caused by differences in genotype among individuals is termed genotypic variance whereas the variation in phenotype caused by differences in environment among individuals is termed environmental variance. Genetic by environment interactions can be defined as the difference between the phenotypic value and the value expected from the corresponding genotypic and environmental values (Baker 1988). Genetic by environment interactions is the variation caused by the joint effects of genotypes and environments (Dickerson 1962). Genetic by environment interactions are great interest when evaluating the stability of breeding plants under different environmental conditions. The reliability of genotype performance across different environmental conditions can be an important consideration in plant breeding. Breeders are primarily concerned with high yielding and stable cultivars as much possible as since cultivar development is a time-consuming endeavor. A successfully developed new cultivar should have a stable performance and broad adaptation over a wide range of environments in addition to high yielding potential.

Evaluating stability of performance and range of adaptation has become increasingly important for breeding

programs. Hence, if cultivars are being selected for a large group of environments, stability and mean yield across all environments are important than yield for specific environments (Piepho 1996). All performance stability, phenotypic stability, and adaptation terms are usually used in total various meanings and different senses and explanations are introduced over the years (Becker and Leon 1988). In a static mean of stability defined by Becker and Leon 1988, a stable genotype is the one possessing a constant performance irrespective of any changes in environmental conditions. Phenotypic stability is often used to refer to fluctuations in the phenotypic expression of yield while the genotypic composition of the varieties or populations remains stable. In the final stage of plant breeding, the new varieties are grown under different seasons of the year, environments, climatic and soil conditions (Becker and Leon 1988; Acciarsi and Chidichimo 1999). The main aim of plant breeder is developing wide adaptive crop. However, developing wide adaptive crop is challenging and needs knowledge of genotype-environment interaction.

The idea that genotype by environment interaction could be considered as the pleiotropic effect of particular variants across environments implies that any given trait when evaluated across more than one environment can be analyzed as genetically correlated traits (Malosetti, *et al.*, 2013). Light, temperature, water and soil greatly influence plant growth and geographic distribution. These factors determine the suitability of a crop for a particular location, cropping pattern, management practices, and levels of inputs needed (Yang, *et al.*, 2016). A crop performs best and is least costly to produce if it is grown under the most favourable environmental conditions. To maximize the production of any crop, it is important to understand how these environmental factors affect plant growth and development (Sarker, *et al.*, 2017). Dry matter production often increases in direct proportion to increasing amounts of light (Ali, *et al.*, 2015). The amount of sunlight received by plants in a particular region is affected by the intensity of the incoming light and the day length. Plant growth and geographic distribution are greatly affected by the environment. All organisms living on earth develop variations due to either genetic effect, environmental effects and both, as a result change in the genetic sequence due to genetic effects is defined as the genetic variation whereas the variation due to environmental effects is defined as the environmental variation (Yash, *et al.*, 2015). The objective of the paper was to understand genotype-environment interaction and stability analysis in crop improvement to develop superior crop variety for different agro-ecologies.

Genotype by environment interaction

Genotype by environment interaction is defined as a phenomenon that phenotypes respond to genotypes differently according to different environmental factors (Hussein, *et al.*, 2000). The concept of genotype-environment interactions leads to measure the agronomic stability of the genotype and under the biological concept stable genotype is one, whose phenotype shows little deviation from the expected character level when performance of genotype is tested over a number of environments. Genotype by environment interaction is an

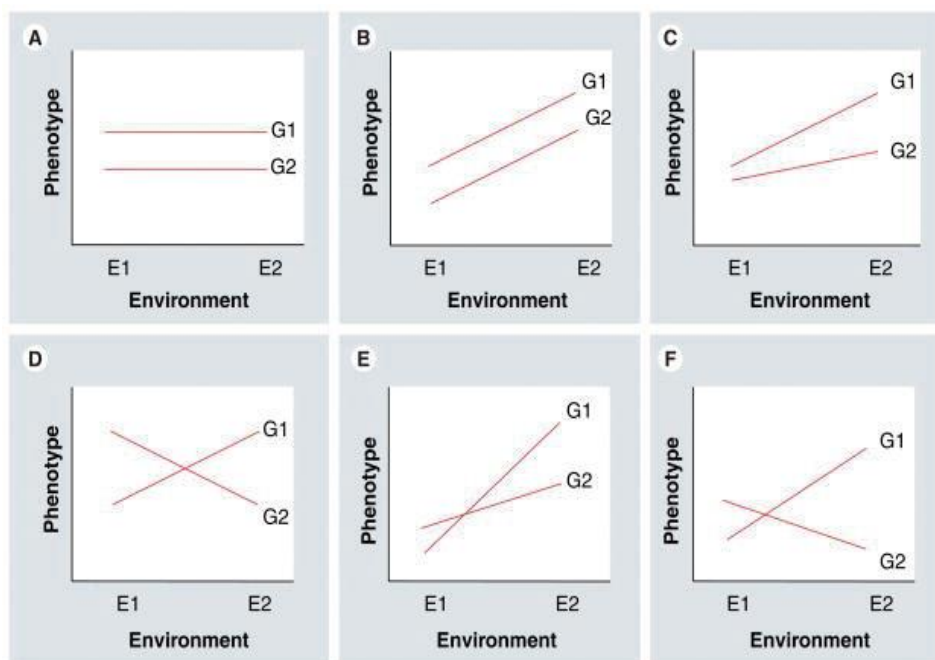


Fig. 1: Graphical representation of the “no” interaction, non-crossover interaction, and crossover interaction types of genotype-environment interactions: Source: Guntrip and Sibly, 1997

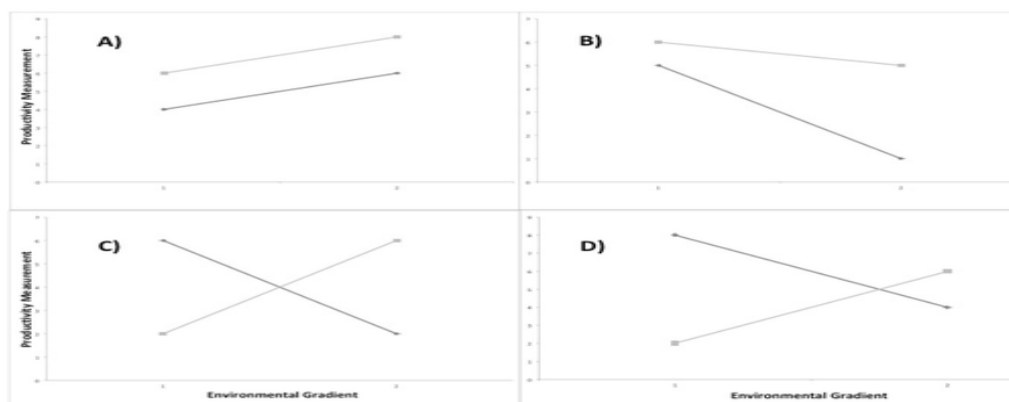


Fig. 2: Examples of different types of interaction between two genotypes and two environments: Source: Leon, *et al.*, 2016

important issue in improvement that affects the consistence performance of genotypes across environments. Genotype-by-environment interaction is a universal issue. The genotype by environment interaction and stability of performance are expected to become more relevant issues as greater emphasis is placed on sustainability of agricultural systems (Hussein, *et al.*, 2000).

Genotype by environment interaction is available when different cultivars respond differently to diverse environments and genotype by environment interaction effects is detected via statistical procedures and at least two genotypes must be evaluated in at least two environments. Genotype by environment interaction is observed in multi-environment trials that genotype performance varies across environments resulting in variation and rank changes among genotypes (Nicolas, *et al.*, 2013). Genotypes by environment interactions are common for most quantitative traits such as yield, plant height and weight of economic importance. Grain yield stability is influenced by the capacity of a genotype to react to environmental conditions, which is determined by the genotype’s genetic

composition. The adaptability and stability of a genotype are useful parameters for recommending cultivars for known cropping conditions. Genotype by environment interaction is the main challenges to improve genotypes because it complicates the selection of superior genotypes by reducing the genetic progress.

A genotype by environment interaction 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 (Natalia de Leon, *et al.*, 2016). The concept that phenotype represents the consequence of genotype by environment interactions is universal and relates to all living organisms. Genotype by environment interactions can be defined as the difference between the phenotypic value and the value expected from the corresponding genotypic and environmental values (Baker 1988).

A conceptual genotype by environment interaction is commonly depicted as the slope of the line when genotype performance is plotted against an environmental gradient. Non-parallel, but nonintersecting lines indicate that the

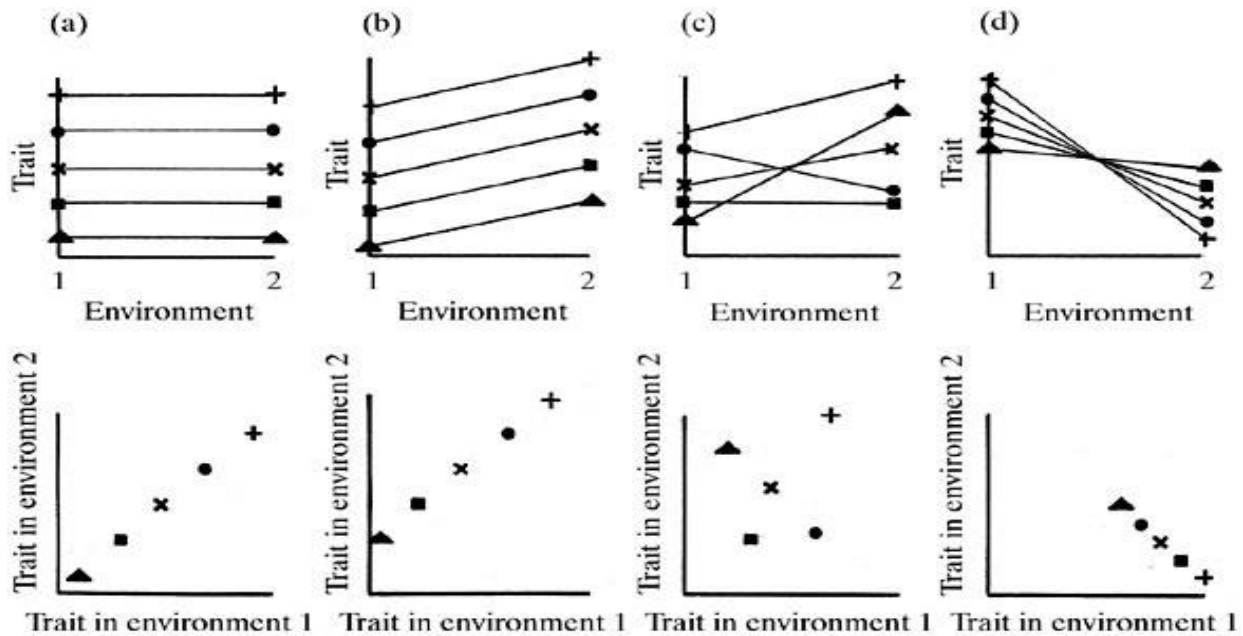


Fig. 3: Phenotypic plasticity, genotype-by-environment interaction and the analysis of generalism and specialization in *Callosobruchus maculatus*. Reaction norms for five genotypes (top row). Each line connects the value of a genotype’s life-history trait in one environment to its value in the other; 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 and Sibily, 1997.

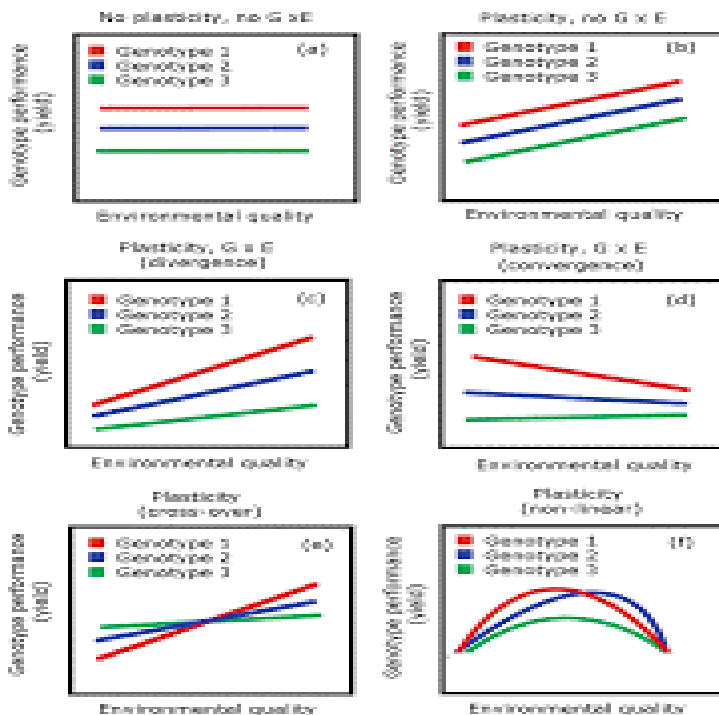


Fig. 4: Genotype-by-Environment Interactions: Source: Marcos *et al.* (2013).

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. G X E 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 (Leon, *et al.*, 2016). Genotype by environment interaction can also be conceptualized as a measurement of the relative plasticity

of genotypes in terms of the expression of specific phenotypes in the context of variable environmental influences (Leon, *et al.*, 2016). Genotype-by-environment interaction is a universal issue that relates to all living organisms, from humans to plants to bacteria (Annicchiarico and Perenzin 1994).

Types of genotype x environmental interaction

Multilocation trials are usually performed by researchers to evaluate new or improved genotypes across multiple environments (locations and years), before they

are promoted for release and commercialization. This is systematic approach undertaken to increase yield stability of new crop varieties in stress-prone environments. The genotype \times environment interaction reduces the association between the phenotypic and genotypic values and leads to bias in the estimation of gene effects and combining ability for various characters that are sensitive to environmental fluctuations less reliable for selection.

Genotype \times environment interactions can be classified into three broad types. (i) No genotype \times environment interaction, (ii) non-crossover interaction, and (iii) crossover interaction. The number of environments (E) and the number of genotypes (G) determine the number of genotypes \times environment interactions possible and that, the higher the number of environments and genotypes the greater the number of possible G \times E interactions. Thus, with two genotypes and two environments, and with only a single criterion, at least four different types of interactions are possible. With 10 genotypes and 10 environments, 400 types of interactions are possible, which would undoubtedly make their implications and interpretation more difficult to comprehend.

Crossover (Qualitative) Interaction

The differential response of cultivars to diverse environments is referred to as a crossover interaction and during crossover interaction, cultivar ranks change from one environment to another environment. The main characteristics of crossover interaction is intersecting lines in a graphical representation. If the lines don't intersect, there is no crossover interaction (Kang 1998). In crop breeding, the crossover interaction is more important than non-crossover interaction, since the presence of a crossover interaction has strong implications for breeding for specific adaptation and it is important to assess the frequency of crossover interactions (Singh, *et al.*, 1999). Variation among genotypes in phenotypic sensitivity to the environment may necessitate the development of locally adapted varieties (Falconer 1952). If no one genotype has superiority in all environments, genotype-environmental interaction indicates the potential for genetic differentiation of populations under prolonged selection in different environments (Via 1984). The differential responses of genotypes to diverse environments when genotype ranks change from one environment to another are referred to as crossovers or qualitative interaction (Cornelius, *et al.*, 1996). The differential and non-stable response of genotypes to diverse environments is referred to as a crossover interaction when the ranks of genotype changes or switch from one environment to another (Haldane 1946). Crossover interaction implies that no genotype is superior in multiple environments (Via 1984).

Non-crossover (Quantitative) Interaction

Non-crossover interaction represents change in magnitude of genotype performance (quantitative), but rank order of genotypes across environments remains unchanged. In this interaction, genotypes that are superior in one environment maintain their superiority in other environments (Ulaganathan, *et al.*, 2015). Non-crossover interactions may mean that genotypes are genetically heterogeneous but test environments are more or less homogeneous or that genotypes are genetically

homogeneous but environments are heterogeneous. All identical genotypes grown in constant (ideal) environments should perform consistently. A non-crossover genotype-environmental interaction is said to occur when one genotype (G_1) consistently outperforms another genotype (G_2) across the test environment.

No genotype-environmental Interaction

When there is no genotype by environment interaction, the effects of each of the risk factors are consistent (homogeneous) across the levels of the other risk factors. A 'no' genotype by environment interaction occurs when one genotype (G_1) consistently performs better than the other genotype (G_2) by approximately the same amount across both environments. There is no genotype by environment interaction when the relative performance among genotypes remains constant across environments.

The G \times E (V_{GE}) displayed here illustrates two components, homogeneity vs. heterogeneity of the genetic variance (V_G) and the correlation between performances across environment. (A) Homogeneity of V_G and no correlation between environments; (B) Heterogeneity of V_G in different environments and no correlation between environments; (C) Crossover interactions are due to imperfect correlations between genotypic performance across environments (in this case -1) and here homogeneous V_G ; (D) V_{GE} is due to a combination of heterogeneous V_G and an imperfect correlation between genotypic performance across environments.

Stability Analysis

Stability refers to the ability of a genotype to perform consistently, across a wide range of environments (Kandus, *et al.*, 2010). Stability in the biological (static) sense refers to the ability of genotypes to maintain constant production in different environments, with low variation between them, which is genotypes exhibit "homeostasis". Stability in the agronomic (dynamic) sense indicates that the genotype positively responds to improvements in edaphic-climatic conditions of the environment and can perform above the mean in different locations (Sabaghnia, *et al.*, 2015). The stability of genotypes can be estimated by different univariate and multivariate statistical parameters as suggested by different authors (Becker and Leon 1988). Among the multivariate methods, the additive main effects and multiplicative interaction (AMMI) analysis is widely used for genotype-by-environment interaction investigation. This method has been effective because it captures a large portion of the genotype-by-environment interaction sum of squares; it clearly separates main and interaction effects and often provides meaningful interpretation of data to support a breeding program such as genotype stability (Crossa, *et al.*, 1990).

The concepts of genotype-by-environment interaction and yield stability have been issues to the breeders and biometricians since a long period of time. A significant genotype-by-environment interaction for a quantitative trait is known to reduce the usefulness of the genotype means over allocations or environments for selecting and advancing superior genotypes to the next stage of selection (Pham and Kang 1988). If there were no genotype-by-environment interaction associated with the genotype-environment system relevant to a breeding objective,

selection would be really simplified because the ‘best’ genotype in one environment would also be the ‘best’ genotype for all target environments (Basford and Cooper 1998) and furthermore, the variety trial needs to be conducted at only one location to provide universal results (Gauch and Zobel 1996).

Types of Stability

Static Stability

Stability is referred to as the presence of persistence and constant performance across-environments with no variation among environments for the same genotypes or varieties. It is also defined as non-responsiveness of genotype to increased levels of inputs and performance of a genotype does not change under different environmental conditions.

The effect of $G \times E$ interaction on any trait is observable when genotypes differentially perform across environments (Malosetti, *et al.*, 2013). The $G \times E$ interaction therefore poses a challenge to effective selection during breeding as it can reduce the heritability of traits in different environments (Romagosa, *et al.*, 2009). A genotype with a high mean performance and a low $G \times E$ interaction is usually considered suitable for a larger environment. However, when $G \times E$ interaction is high, genotypes may be selected for local adaptation (Gauch and Zobel 1996). Development of a stable variety is one of the major objectives of all breeding programs. Phenotypically stable varieties are usefully sought for commercial production of crop plants. In any breeding program, it is necessary to screen and identify phenotypically stable genotypes, which could perform more or less uniformly under different environmental conditions.

Dynamic Stability

Dynamic stability implies that a genotype’s performance is stable, but for each environment, its performance corresponds to the estimated or predicted level, which is also referred to as the agronomic concept of stability. Genotype performance is affected by the environment, but its relative performance is consistent across environments.

Multivariate Approaches for Stability Analysis

There are many different multivariate models for stability and adaptability analysis. Among them additive main effects and multiplicative interaction (AMMI) and biplot technique (Gge biplot) are the two most commonly used approaches.

The Additive Main Effects and Multiplicative Interaction (AMMI)

Additive Main Effects and Multiplicative Interaction approach used to measure of stability and adaptability genotype in the presence of genotype-by-environment interaction. Several methods can be used to examine genotype-by-environment interaction (Malosetti, *et al.*, 2013) and these include components of variance analysis, stability analysis, as well as qualitative and multivariate analysis (Becker and Leon 1988). However, the additive main effects and multiplicative interaction (AMMI) method is one of the most widely used (Malosetti, *et al.*, 2013). The AMMI model combines ANOVA for the genotype and environment main effects with principal components analysis of genotype-by-environment

interaction (Zobel, *et al.*, 1988). Additive Main Effects and Multiplicative Interaction (AMMI) analysis interprets the effect of genotype and environment as additive effects plus genotype-by-environment interaction as multiplicative component.

Biplot Technique (Gge Biplot)

The biplot technique named ‘GGE biplot’ was developed by Yan, *et al.* (2000) to represent genotype main effects and genotype-by-environment interaction graphically. Although biplot analysis is not sensitive to the number of genotypes but it is the best predictor of genotype stability for a small number of genotypes (Rose, *et al.*, 2008). The yield of a genotype in an environment is a mixed effect of genotype main effect (G), environment main effect (E) and GE. Simultaneous examination of genotype and genotype-by-environment interaction is an important principle in cultivar evaluation. Although AMMI and GGE are equivalent in achieving predictive accuracy and the AMMI method is considered superior to GGE for evaluating yield trial data (Gauch, *et al.*, 2008), because it shows genotype main effects, environment main effects and interaction effects, whilst the GGE biplot only displays G and $G \times E$ effects (Gauch *et al.*, 2008).

Importance of Genotype-by- Environment Interaction

Genotype \times environment (GXE) interactions is important in the development and evaluation of plant varieties because they reduce the genotypic-stability values under diverse environments (Hébert, *et al.*, 1995). The phenomenon of genotype \times environment interaction refers to the differential performance of genotypes in different environments that affect the efficiency of selection in a breeding program. Genotype \times environment interactions arises due to the differences in the sensitivities of genotypes to the different environmental conditions. In order to mitigate the effect of $G \times E$ interaction, crops need to be tested in several environments to assess their specific and broad adaptation. Plant productivity is a direct consequence of how well adapted the genotype of an individual is to the surrounding environment. Genotype-by-environment interaction is the interest to plant breeders for several reasons (Fehr 1987). Living organisms are made up of genes whose expression are subject to modification by the environment; therefore, genotypic expression of a phenotype is environmentally dependent.

Genotype \times environment interaction effect complicates the selection of suitable varieties by breeders because elite varieties developed for one location may not perform the same in different locations. Breeding of crops involves different attributes of the genetic materials that are subject to variation in environmental conditions. To mitigate the confounding effect of $G \times E$ interaction on selection efficiency, plant breeders have devised strategies to ensure progress in selection efficacy. An understanding of the genotype stability across environments helps in determination of their suitability for the fluctuations in growing conditions that are likely to be encountered, integrated utilization of multi-environment trial data, pedigree information and genotypic data of cultivars and for improving accuracy and precision in the assessment of both genetic and environmental influences. Several methods have been developed and applied by plant

breeders to explain the genotype \times environment interaction at the end of plant breeding programs.

Cultivar development based on the assessment of the phenotypic values of different genotypes under varying environmental conditions is needed to select high-yielding and stable varieties (Marfo and Padi 1999). However, genotypes tested in different locations or years often produce significant varying results in performance due to differences in response to factors such as soil fertility and presence of pathogens (Padi 2008). This differential performance referred to as genotype \times environment ($G \times E$) interaction can complicate a genotype's ability to demonstrate superior performance across environments (Romagosa, *et al.*, 2009). Thus, the genotype \times environment interaction can result in low correlation between phenotypic and genotypic values, leading to a bias in heritability estimates and a slowdown in selection progress (Romagosa, *et al.*, 2009).

In essence, the $G \times E$ interaction usually determines the optimum breeding strategy to adopt (Romagosa, *et al.*, 2009). Yield stability is influenced by the capacity of a genotype to react to environmental conditions, which is determined by the genotype's genetic composition (Ulaganathan, *et al.*, 2015). The basic cause for difference in the performance of genotypes over environments is the occurrence of genotype-environment interaction (Gedif and Yigzaw 2014). In varying environments, it may be expected that the interaction of genotype with environment will also be varying and ample. As a result, one cultivar may have the highest yield in one environment, while a second cultivar may excel in others. This necessitated the study of genotypes by environment interaction to know the magnitude of interactions in the selection of genotypes across several environments besides calculating the average performance of the genotypes under evaluation (Chandrakanth, *et al.*, 2016).

Summary and conclusion

Genotype by environment interaction is defined as a phenomenon that phenotypes respond to genotypes differently according to different environmental factors. The genotype \times environment interaction has been an important and challenging issue among plant breeders, geneticists, and agronomists engaged in performance testing. The genotype \times environment interaction reduces association between phenotypic and genotypic values and leads to bias in the estimates of gene effects and combining ability for various characters that are sensitive to environmental fluctuations. Breeders and geneticists continually strive to broaden the genetic base of crop species to prevent problems associated with genetic vulnerability. With emphasis on broadening the genetic base and unpredictable climatic factors encountered at different sites and years, differential responses are expected of improved cultivars-strains in different environments. These differential genotypic responses to different environments are collectively called genotype-by-environment interaction.

Development of new genotypes with high yield and acceptable level of stability is an important breeding program. 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 success of a variety depends not only on its high yielding potential but also on the stability of its yield over years across environments. If a variety gives high and stable performance over years at a location within an agro-climatic zone, it is called a stable variety. When the same variety is grown in different agro-climatic regions and if it shows high yield with little or no change in performance in comparison to other varieties, it is called a widely adapted variety. The adaptability, thus refers to the reduced variation in performance across locations, whereas stability refers to the reduced variation in performance across years.

Genotype by environmental interaction is the variation caused by the joint effects of genotypes and environments. Developing wide adaptive crop depends on the knowledge of genotype environment interaction and proper stability analysis. Generally, genotype \times environmental interaction is a prerequisite for crop plant improvement and evaluates the improved genotypes across multiple environments (locations and years), before they are promoted for release and commercialization. The genotype by environment interaction results in non-stable performances between the genotypes across environments. Thus, significant $G \times E$ results from the changes in the degree of differences between genotypes in diverse environments or changes in the relative ranking of the performance of the genotypes. Genotype \times environment interaction is one of the main challenges in the selection of broad adaptation and stable genotypes in most breeding programs. Therefore, evaluation of genotypes for adaptation and stability is the key prerequisite to proceed to another improvement programs.

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