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Review on Genotype X Environment Interaction in Plant Breeding and Agronomic Stability of Crops

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Abstract
G×E is defined as a phenomenon that phenotypes respond to genotypes differently according to different environmental factors. 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. 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. The method commonly used for analysis of G×E interaction is the Linear Regression model in which the bi-values give information about adaptability and S2d is used as measure of stability of performance, AMMI (Additive Main Effects and Multiplicative Interaction) approach as a measure of stability and adaptability and etc. Plant productivity is a direct consequence of how well adapted the genotype of an individual is to the surrounding environment. This and different issues concerning G X E was reviewed.
Keywords: Genotype, Environment, Interaction, Plant breeding, Stability

1. Introduction

All organisms living on earth develop variations due to either genetic effects or environmental effects or both, as a result change in the genetic sequence due to genetic effects is defined as the genetic variation and the variation due to environmental effects is defined as the environmental variation (Yash, 2015). 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 (Disharee and Tapash, 2013*)*. It is also well recognized that environmental factors can influence levels of DNA methylation and alter chromatin states. Such epigenetic modulation has been proposed as a mechanism affecting plasticity levels of specific plant genotypes across environments (Mittelsten, 2012; Zhang et al., 2013 and Leon *et al*., 2016).

The idea that G X E 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). In this case, the magnitude of such a correlation indicates the degree of shared genetic control and the sign of the correlation indicates the direction of the allelic effect for the environments being considered. This perspective has provided an important framework for interpreting and handling G X E in plant breeding programs (Marais *et al*., 2013). As with most other areas of quantitative genetics, this has led to the development of statistical as opposed to biological parameters to quantify, understand, and interpret G XE in plant breeding (Malosetti *et al*., 2013).

2. Body

2.1. Definition and Importance of G X E

G×E is defined as a phenomenon that phenotypes respond to genotypes differently according to different environmental factors (Kim. *et al., 2014*). A conceptual G X E 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. 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).

Two different categories of interaction can occur and are defined as follows: qualitative or crossover interactions–change in ranks of genotypes from one environment to another whereas non-rank change interactions are called quantitative or non-crossover interactions (Leflon *et al*., 2015). G X E 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. Although a clear divide characterizes the long and rich history of the scientific field concerned with phenotypic plasticity, one foundational understanding has

united researchers across disciplines: the ability of genotypes to express different phenotypes when influenced by different environmental signals has a genetic basis (Leon *et al*., 2016).

2.2. Effect of Environment in Quantitative Inheritance

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 (Ulaganathan *et al*., 2015). The basic cause for difference in the performance of genotypes over environments is the occurrence of genotype-environment interaction (GEI) (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 (Chandrika *et al.*, 2015).

2.3. Methods of Measuring G XE

Estimates of the variance components indicated that GXE interactions explained a sizable proportion of the phenotypic variance (Ruud, 2015). The concept of genotype-environment interactions leads to measure the agronomic stability of the genotype. Plant improvement involves jointly the manipulation of genetic characteristics to optimize productivity in relation to the limitations of the environmental factors (Disharee and Tapash, *2013)*. The GEI is statistically defined as the difference between the phenotypic value and the value expected from an additive model that considers the general mean as well as genotypic and environmental main effects (Leflon *et al*., 2015). The analysis of GEI requires a good knowledge of the test environments. This method generates many varieties that can be sometimes correlated with each others, reducing their own significance in the statistical analyses of the interaction and decreasing the efficiency of the models (Leflon *et al*., 2015). Crop diagnosis then allows to determine the most important yield-limiting factors of the environment, and to integrate only these factors in further analyses of the interaction for the other tested genotypes (Leflon *et al*., 2015). Therefore, this method implies: to choose relevant probe genotypes; estimate for each environment, the deviations (or losses) of yield as well as deviations of yield components, relative to the chosen probe genotypes, by a comparison to their reference values and to relate these deviations of yield and yield components to the environmental characteristics. The method commonly used for analysis of G×E interaction is the Linear Regression model of (Eberhart and Russell, 1966), in which the bi-values give information about adaptability and S2d is used as measure of stability of performance. Other workers (Zobel *et al*., 1988), suggested the use of AMMI (Additive Main Effects and Multiplicative Interaction) approach as a measure of stability and adaptability. The AMMI model is a better model for analysis of GxE interaction in multiplication varietal trials (Zobel *et al*., 1988). It does not only give estimate of total GxE interaction effect of each genotype but also partitions it into interaction effects due to environments (Abuali. *et al*., 2014). To evaluate the interaction effects, the data were subjected to stability analysis following the AMMI model. The AMMI model is a hybrid statistical model incorporating both ANOVA (for additive component) and PCA (for multiplicative component) for analyzing two way (genotype x environment interaction) data structures (Abate, 2015). The ranking of seven wheat-barley DALs and the two parents based on their mean yield and stability performance are shown in Fig. 2. The line passing through the biplot origin is called the average tester coordinate (ATC), which is defined by the average PC1 and PC2 scores of all environments (Yan and Kang, 2003). More close to concentric circle indicates higher mean yield. The line which passes through the origin and is perpendicular to the ATC with double arrows represents the stability of genotypes. Either direction away from the biplot origin on this axis indicates greater GE interaction and reduced stability. For selection, the ideal genotypes are those with both high mean yield and high stability. In the biplot, they are close to the origin and have the shortest vector from the ATC. The DALs H2, followed by H4, can be considered as genotypes with both high yield and stability performance. The other genotypes on the right side of the line with double arrows have yield performance greater than mean yield and the genotypes on the left side of this line had yields less than mean yield. The genotypes with highest yielding performance but low stability were H7 and H3, whereas the genotypes with low yield and low stability were the both parents (CS, Betzes). The DALs of H4 (with relatively high yield) and H1 (with lowest yield) were similar in GE interaction. Breeders can also use Fig. 1 for selecting the genotypes with the best response to particular environments.

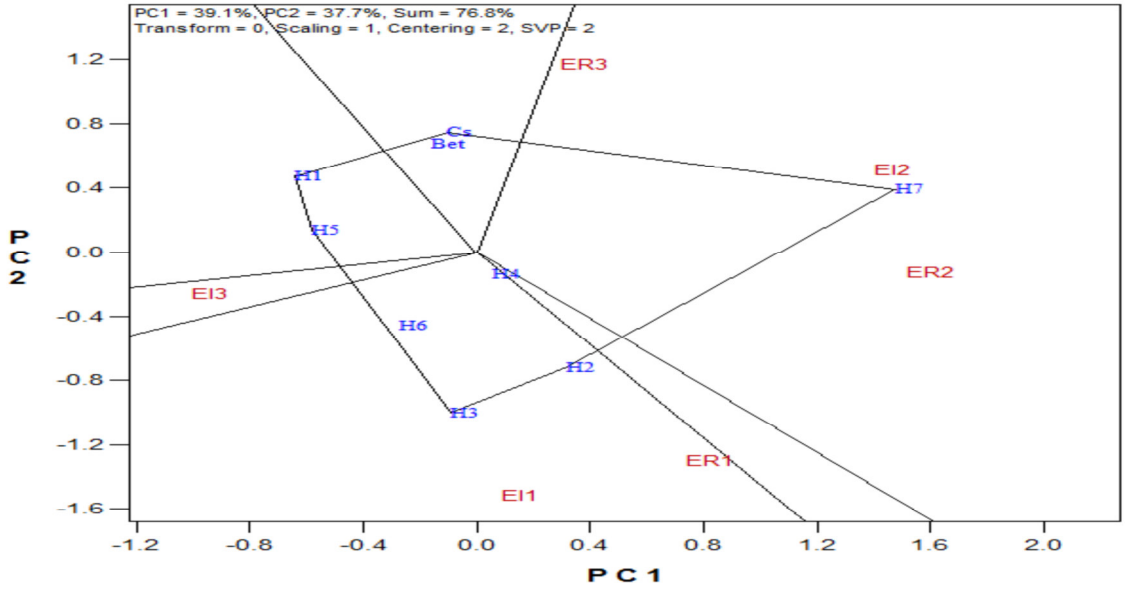


Figure 1. Polygon view of genotype- environment interaction for wheat-barley disomic addition lines over six test environments. The vertex genotype in each sector is the best genotype at environments whose markers fall into the respective sector. Environments within the same sector share the same winning genotype, and environments in different sectors have different winning genotypes. H1-H7 is the codes for the wheat-barley disomic addition lines and CS and Bet are the recipient and donor parents, respectively. ER1, ER2 and ER3 are environmental codes for the environments under rain fed conditions in 2009, 2010 and 2011 cropping seasons, respectively. EI1, EI2 and EI3 are environmental codes for the environments under irrigated conditions in 2009, 2010 and 2011 cropping seasons, respectively. Source: Farshadfar *et al*., 2012

Table 1. Analysis of variance for grain yield of seven disomic addition lines and two parents across six growing conditions

Source	Df	Ms	SST
Genotype (G)	8	973.37**	15.6
Environment (E)	5	2699.73**	27.1
Interaction (GE)	40	713.06**	57.3

2.4. Multi-Location Trial

The most recent method GGE bi-plot model provides breeders with a complete and visual evaluation of all aspects of the data by creating a bi-plot that simultaneously represents both mean performance and stability, optimized environments for specific genotypes and identifies mega-environments (Gedif and Yigzaw, 2014). Most of the evaluations of the effect of the environment on performance in plant breeding have relied on multi-environmental field testing that represent target production environments and those are used to identify and develop cultivars (Leon *et al*., 2016 cited from Comstock, 1977). These multi-location studies provide two-way tables of means for diverse genotypes across different environments (Leon *et al*., 2016). 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. This provides a good indication of the proportion of the variance that refers to the main effect of genotype compared to G XE, 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) and modified by others (Eberhart and Russell, 1966) which qualified G X E based on the slope of the regression of the performance of particular genotypes across an environmental gradient (Leon *et al*., 2016).

2.5. Variation and Its Components

2.5.1. Phenotypic Variation

The ability of an individual to achieve the maximum potential encoded in its genome is a function of the environment in which it completes its life cycle while expression of a phenotype is a function of the genotype, the environment and differential phenotypic response of genotypes to different environments, also known as genotype by environment (G X E) interaction (Leon *et al*., 2016).

2.5.2. Environmental Variation

Relation among test environments**:** GGE (G +GE) biplot which depends on environment focused scaling was

portrayed to estimate the pattern of environments. To visualize the relationship between environments, lines were drawn to connect the test environments to the biplot origin known as environment vector. The cosine of the angle between the two environments is used to approximate the relation between them. Thus, positive correlations were found between test seasons (years) in a location as the angle between them was less than 90 (Gedif and Yigzaw, 2014). Individuals with the same genotype may develop variation due to different environmental conditions and sometimes, strong environmental variations affect the genotype while most of the environmental variations affect phenotype (Yash, 2015).

2.5.3. Genotypic Variation

Historically breeders have recognized the potentially negative implications of G X E in selection and cultivar deployment and have focused on developing tools and resources to quantify it as a first step toward minimizing its detrimental effect and, whenever possible, taking advantage of positive interactions (Cooper et al., 2014; Sadras and Richards, 2014). Commonly, target cultivars are identified for deployment to specific sets of environments (Leon *et al*., 2016). That identification ideally proceeds from the interpretation of analyses that measure the differential sensitivity of genotypes to environments and that connect that variation to particular biological mechanisms (Sadras and Richards, 2014). A proportion of the G X E studies have used managed stress trials to emphasize the effect of particular sources of, generally, a biotic stresses on the performance of diverse genotypes (Leon *et al*., 2016). The genotypes, which were found to be stable on the basis of the approach of stability analysis for all or most of the characters, were considered to be highly stable.

2.5.4. Components Genotypic Variation

vp=vg+ ve = {vD+vH+vI}+vE

VP = phenotypic variation; Vg=genotypic variation [D=additive gene effect H= dominance gene effect and I=variance due to epistatic gene effects] and Ve = environmental variation

2.5.4.1. Additive Gene Effect

Additive genetic effects are the contributions to the final phenotype from more than one gene, or from alleles of a single gene (in heterozygotes), that combine in such a way that the sum of their effects in unison is equal to the sum of their effects individually. Genetic effects that are not additive involve dominance (of alleles at a single locus) or epistasis (of alleles at more different loci).

2.5.4.2. Dominance Gene Effect

Dominance in genetics is a relationship between alleles of one gene, in which the effect on phenotype of one allele masks the contribution of a second allele at the same locus. The first allele is dominant and the second allele is recessive. For genes on an autosome (any chromosome other than a sex chromosome), the alleles and their associated traits are autosomal dominant or autosomal recessive. Dominance is a key concept in Mendelian inheritance and classical genetics. Often the dominant allele codes for a functional protein whereas the recessive allele does not (https://en.wikipedia.org/wiki/Dominance_(genetics).

2.5.4.3. Epistatic Gene Effects

Regarding the definition of epistasis, this term was initially described by Bateson (1909) to explain the observed deviation from the expected Mendelian segregation, where an allele from a particular locus might interact with other alleles at different loci. In other words, instead of occurring only in intra-locus interactions, Bateson suggested that alleles from different loci may interact with each other to under- or over express particular genes. Currently, there are different interpretations of epistasis and these divergences have caused some confusion for example, geneticists have used the term “epistasis” to describe three different events: i) the functional relation among two or more genes, ii) genetic ordering in regulatory pathways and iii) deviation from the additivity in the effect of alleles at different loci in relation to their contribution to a quantitative phenotype (Balestre and Souza, 2016).

2.6. Stability and Adaptability under G XE Interaction

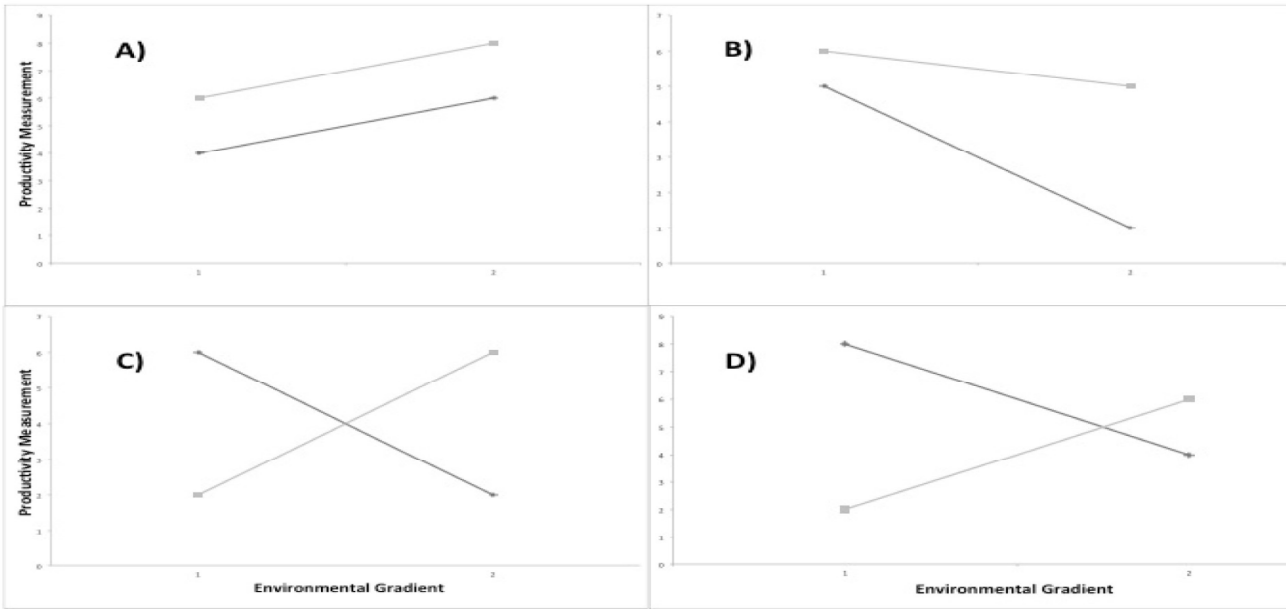
The plant breeder is always interested in the stability of performance for the characters which are of economically important. The desirable hybrids should have low g x e interactions for important characters, so as to get desirable performance of hybrids over wide range of environmental conditions. Genotype x environment interactions are of common occurrence and often creates manifold difficulties in interpreting results and thus hamper the progress of breeding programmes aiming at further genetic improvement in crop plants (Chandrika *et al.*, 2015). 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. A univariate nonparametric stability methods are not affected by data distribution and these methods are based on rank order of genotypes, a genotype is considered stable if its ranking is relatively constant across environments (Temesgen *et al*., 2015). Analysis of interaction of genotypes with locations and other agro-ecological conditions would help in getting information on adaptability and stability of performance of genotypes (Abuali *et al*., 2014). An ideal genotype should have both high mean yield performance and high stability across environments (Gedif and Yigzaw, 2014).

The adaptability and stability of a genotype are useful parameters for recommending cultivars for known cropping conditions. Eberhart and Russell (1966), proposed an assessment of cultivar response to environmental changes using a linear regression coefficient and the variance of the regression deviations. Therefore, the genotypes with regression coefficients greater than one would be more adapted to favorable growth conditions; those with regression coefficients less than one would be adapted to unfavorable environmental conditions, i.e., to the water stress environments, and those with regression coefficients equal to one would have an average adaptation to all environments. Thus, genotypes with variances in regression deviations equal to zero would have high stability, whereas those with a variance of deviation from regression greater than zero would have low stability (Abuali. *et al*., 2014). AMMI analysis of variance for ten sesame varieties tested in six environments showed that the mean squares for genotypes, environments and GEI were highly significant for the studied traits (Table 2), indicating the existence of differential responses of varieties to different environments and suggests the need for the extension of G x E analysis.

Table 2. Pooled AMMI analysis of variance for sesame yield and its components over three locations and two different seasons (2010/11 & 2011/12)

		Mean Squares		
Source of variation	**DF**	**SYPL**	**HIPL**	**CPPL**
Treatment	59	12.78**	1545.00**	16348.00**
Genotype	9	33.40**	2353.00**	70595.00**
Environment	5	49.53**	10821.00**	46114.00**
Rep within Env	12	1.27	171.00	1329.00
G X E	45	4.58**	353.00**	2191.00*
IPCA 1	13	9.84**	451.00**	3773.00*
IPCA 2	11	3.40*	499.00**	2109.00*
Error	108	1.94	215.00	2011.00
Gr. Mean		8.26	51.23	296.7
C.V. (%)		16.7	26.8	15.1

Note: **, * significant in 1% and in 5% probability respectively, DF = degree of freedom, SYPL = seed yield per plant, HIPL = harvest index per plant, CPPL= No of capsules per plant Source: Abate, 2015



Source: Leon *et al.*, 2016

Figure 2. The G x E (*V*GE) displayed here illustrates two components, homogeneity vs. heterogeneity of the genetic variance (*V*G) and the correlation between performance 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

Table 3. Effect of geographical location and genotype on yield components of tea plant

	Shoot growth rate (mm/day)				Shoot dry weight (g/shoot)				Shoot density (shoots/m^2)				Shoot water potential (KPa)			
Clone	Tmbl	Kgta	Kpkb	Clone mean	Tmbl	Kgta	Kpkb	Clone mean	Tmbl	Kgta	Kpkb	Clone mean	Tmbl	Kgta	Kpkb	Clone mean
TRFK 7/3	0.45	0.35	0.85	0.55	0.25	0.12	0.16	0.17	32.83	96.25	72.89	67.32	−9.92	−10.06	−10.61	−10.20
TRFK303/577	0.52	0.35	0.96	0.61	0.22	0.11	0.15	0.16	45.00	119.25	71.44	78.56	−9.09	−10.83	−10.32	−10.08
AHPTN 14-3	0.59	0.28	1.12	0.66	0.28	0.12	0.16	0.19	39.08	92.75	68.33	66.72	−9.89	−10.69	−9.80	−10.13
TRFK 2X1/4	0.53	0.32	0.84	0.56	0.23	0.09	0.14	0.15	35.83	86.75	75.56	66.05	−9.94	−10.77	−9.82	−10.18
STC 5/3	0.54	0.30	0.70	0.52	0.23	0.09	0.14	0.15	32.42	98.08	79.78	70.09	−9.80	−10.83	−10.33	−10.32
TRFK 11/26	0.35	0.34	0.65	0.44	0.18	0.12	0.16	0.15	33.92	84.25	71.22	63.13	−10.10	−10.52	−9.48	−10.03
TRFK 12/19	0.39	0.27	0.62	0.42	0.21	0.13	0.15	0.16	32.16	79.00	74.44	61.87	−10.18	−11.37	−10.32	−10.62
TRFK 56/89	0.73	0.37	0.92	0.67	0.33	0.14	0.14	0.21	40.16	83.50	64.11	62.59	−10.17	−10.60	−9.73	−10.17
TRFK 12/12	0.36	0.32	0.56	0.41	0.22	0.17	0.17	0.19	38.00	79.25	65.44	60.90	−9.81	−9.63	−10.34	−9.93
TRFK 303/999	0.53	0.42	0.77	0.57	0.26	0.12	0.17	0.18	42.50	79.92	68.33	63.58	−9.79	−10.80	−10.58	−10.39
S 15/10	0.29	0.36	0.74	0.46	0.25	0.13	0.18	0.19	35.08	90.25	70.78	65.37	−10.13	−11.22	−10.22	−10.53
TRFK 57/15	0.38	0.37	0.92	0.56	0.18	0.09	0.17	0.15	44.08	93.58	68.00	68.55	−10.20	−11.31	−10.32	−10.61
31/27	0.30	0.38	0.73	0.47	0.28	0.12	0.15	0.18	32.75	89.33	74.89	65.66	−10.19	−10.59	−10.19	−10.32
TRFK 6/8	0.32	0.37	0.58	0.42	0.24	0.13	0.16	0.18	30.25	81.25	71.00	60.83	−9.51	−9.91	−10.26	−9.89
BB 35	0.48	0.40	0.83	0.57	0.24	0.11	0.16	0.17	32.83	89.58	71.11	64.51	−9.80	−9.80	−9.90	−9.83
TRFK 31/8	0.45	0.28	0.80	0.51	0.26	0.13	0.18	0.19	48.58	80.67	71.55	66.93	−10.00	−10.82	−9.96	−10.26
TRFK 7/9	0.39	0.34	0.60	0.44	0.30	0.11	0.14	0.18	39.66	93.25	76.11	69.67	−10.62	−10.87	−10.38	−10.62
TRFK 303/259	0.39	0.32	0.80	0.50	0.25	0.15	0.16	0.19	53.50	75.58	67.11	65.40	−10.53	−10.16	−10.19	−10.29
TRFK 303/1199	0.64	0.31	0.76	0.57	0.27	0.10	0.14	0.17	41.42	103.50	73.55	72.82	−10.64	−10.61	−10.21	−10.49
TRFK 54/40	0.36	0.34	0.65	0.45	0.16	0.17	0.16	0.16	34.58	74.00	71.11	59.90.	−10.58	−10.62	−10.19	−10.46
Site mean	0.44	0.34	0.77		0.24	0.12	0.16		43.03	94.47	71.15		−10.04	−10.60	−10.16	
CV%		33.97				23.9				22.65				22.65		
	Cl	St	ClxSt		Cl	St	ClxSt		Cl	St	ClXSt		Cl	St	ClxSt	
LDS (P < 0.05)	0.81	0.31	0.14		0.024	0.0094	0.042		8.4	3.25	14.56		NS	0.25	14.56	

Cl = clone; St. = site Source: Nyabundi *et al*., 2016

Promising genotypes need to be evaluated in multi-environmental test over several years for identification of the stable and widely adapted genotypes as a result, a significant g X e interaction may be either crossover, in which a significant change in rank occurs from one environment to others, or a non-crossover g X e interaction, in which the ranking of genotypes remains constant across environments and the interaction was significant because of change in the magnitude of response (Disharee and Tapash, 2013). Plant productivity is a direct consequence of how well adapted the genotype of an individual is to the surrounding environment. Useful phenotypic characterization is therefore location-specific and represents the integration of the entire lifecycle of the plant and the local environmental conditions. To truly increase efficiency in agricultural production, a key component will be to predict accurately the performance of specific genotypes across a wide range of variable environments (Leon *et al*., 2016). Differences in genotype stability and adaptability to environment can be qualitatively assessed using the biplot graphical representation that scatters the genotypes according to their principal component values (Abate, 2015). Tea shoot densities showed significant ($p \leq 0.001$) variations due to genotype and location. The genotype x location interactions was also significant ($p \leq 0.001$). Whereas shoot dry weights varied ($p \leq 0.001$) between sites there was no apparent response to temperature or vapour pressure deficit. The shoot densities variation ($p \leq 0.001$) due to location however, correlated positively with vapour pressure deficits but not temperature, across the sites (table 3). The highest mean shoot density was recorded in Kangaita (119 shoots m−2) and lowest at Timbilil (32 shoots m^{-2})

2.7. G X E Research Results of Some Crops

According to (Abuali *et al*., 2014) AMMI analysis for maize grain yield (kg/ha) revealed that significant difference was detected among the testing environments, genotypes and genotype × environment interaction. The partitioning of GGE through GGE biplot analysis showed that PC1 and PC2 accounted for 51.24% and 20.02% of GGE sum of squares, respectively explaining a total of 71.24% variation this revealed that there was a differential yield performance among potato genotypes across testing environments due to the presence of GEI (Gedif and Yigzaw, 2014). The analysis of variance revealed that though the magnitudes of non linear [environment + (genotype x environment)] components were significant, but were lower in comparison to linear genotype x environment for all the characters except pod length Of Mungbean (Disharee and Tapash, *2013*). Of the total variance of fababean grain yield, environment main effect accounted for 89.27%, whereas genotype and G × E interaction effects accounted for 2.12% and 3.31% of the total variation, respectively according to (Temesgen *et al*., 2015). Grogan et al (2016) analyzed the variation of maturity and yield across environments (i.e., the plasticity of these traits) relative to the trait means in wheat.

3. Conclusions

Plant productivity is a direct consequence of how well adapted the genotype of an individual is to the surrounding environment. Useful phenotypic characterization is therefore location-specific and represents the integration of the entire lifecycle of the plant and the local environmental conditions. To truly increase efficiency in agricultural production, a key component will be to predict accurately the performance of specific genotypes across a wide range of variable environments.

The combination of rich genomic information and detailed environmental assessments allows not only an enhanced ability to quantify and mitigate the unrepeatable portion of G XE, but also to genetically characterize it

in economically important crops in the context of relevant production conditions. Similarly, a deeper understanding of the specific environmental components that generate crossover G X E interactions at specific plant developmental stages is expected to enhance our ability to determine the value of on-the-fly management decisions.

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