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Genotype × Environment Interaction: A Prerequisite for Tomato Variety Development

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Abstract

Tomato (*Solanum lycopersicum* L.) is the second most important vegetable crop in the world due to its high level of nutrition particularly in vitamins and antioxidants. It is grown in several ecologies of the world due to its adaptability and ease of cultivation. Besides field conditions, tomatoes are grown in controlled environments which range from hydroponics and simple high tunnel structures to highly automated screen houses in advanced countries. However, the yield and quality of the fruits are highly influenced by the environment. This results in unpredictable performances in different growing environments in terms of quality, a phenomenon known as genotype by environment ($G \times E$) interaction which confounds selection efficiency. Various approaches are employed by plant breeders to evaluate and address the challenges posed by genotype by environment interaction. This chapter discusses various field and controlled environments for growing tomatoes and the effect of these environments on the performance of the crop. The various types of genotype × environment interactions and their effect of the tomato plant are discussed. Finally, efforts are made to suggest ways and methods of mitigating the confounding effects of genotype × environment interaction including statistical approaches.

Keywords: tomato (*Solanum lycopersicum* L.), adaptability, field conditions, controlled environments, genotype × environment interaction

1. Introduction

The rise in population and the ensuing increase in the demand for agricultural produce are expected to be greater in Africa where production is not adequate. The need for increase in

agricultural production cannot be overemphasized. This embodies challenges to forming systems, and must come mainly from increased yield per unit area, given the limited scope for extension of cultivated land worldwide. To meet this requirement, numerous crop improvement programs all over the world have been initiated. In every crop improvement program, promising genotypes are tested for their performance each year at a number of sites, representing the major growing area of the crop. This is to identify genotypes which possess the dual qualities of high-yield sustainability to adverse changes in environment condition. It is observed that a specified difference in environment may produce disparity outcome on genotype. This interplay of genetic and nongenetic effects causing differential relative performances of genotypes in different environments is called genotype \times environment interaction (GEI). A genotype \times environment interaction thus may perhaps be a change in the relative performance of a character of two or more genotypes measured in two or more environments. There have been early efforts made to classify genotype-environment interactions into four groups [1]. The first group, although was not an interaction, was later observed as a nonadditive relationships between genotype and environment [2].

2. Origin of genotype \times environment interaction

There are two different conceptions of the origin of gene \times environment interaction (GEI). The two concepts are referred to as biometric and developmental interaction [3] or statistical and common sense interaction [4]. Fisher introduced the biometric concept of GEI, whereas Lancelot Hogben introduced the developmental concept of GEI [3]. The biometric (statistical) concept of GEI has its origins in research programs that seek to measure the relative proportions of genetic and environmental contributions to phenotypic variation within populations. Biometric gene \times environment interaction has particular importance in population genetics and behavioral genetics [3]. Developmental GEI is a concept more commonly used by developmental geneticists and developmental psychobiologists. The developmental interaction is not seen merely as a statistical phenomenon, but manifested in the causal interaction of genes and environments in producing an individual's phenotype [5]. Most of the subsequent history of research on GEI has largely been based on the Fisher and Lancelot Hogben's concepts [3].

3. Tomato genome and genetic variation

Tomato (*Solanum lycopersicum* L.) is the second most important vegetable crop in the world, and an important model plant for genetics and genomics studies, because of its relatively short reproductive cycle and small genome size. Moreover, the continued importance of tomato as a vegetable is reflected by the large volume of research on almost all aspects of the crop. Its genotype determines the characters expressed by the crop. The tomato genome has been translated by plant geneticists who discovered that the crop contains 31,760 genes after mapping its genetic makeup. The tomato's genome is, however, closer to that of a potato. As a crop plant, tomato is one of the best-characterized plant systems. It has a relatively small genome of

0.95 pg or 950 Mb per haploid nucleus [6] and features such as diploidy, self-pollination, and a relatively short generation time make it amenable to genetic analysis. The tomato genome at the DNA level consists of approximately 78% single-copy sequences, as evaluated under high stringency hybridization conditions [7]. The remaining part of the tomato sequences is repetitive DNA of which four major classes have been characterized. Ribosomal DNA represents the most abundant repetitive DNA family and comprises approximately 3% of the tomato genome. Both 5S and 45S rRNA genes are tandemly repeated with 1000 and 2300 copies and map to single loci on chromosomes 1 and 2, respectively [8]. Tomato chromosomes can easily be identified by pachytene analysis. With the development of trisomics, monosomics, and translocations through chromosome engineering, tomato cytogenetic research has become one of the most advanced areas in the field of agriculture. Tomato crosses with its wild relatives with varying degrees of difficulty; thus, wild relatives can and have been used as sources of genes for crop improvement. Wild species are interesting resources of genetic variation for introgression breeding and comprise exclusive sources of many resistance genes for cultivated tomatoes [9]. Higher plant densities have increased yield in tomatoes and it is influenced by the genotype [10–16].

4. Tomato growth and environment

Tomato is grown under various environments ranging from field conditions such as gardens and under controlled environments. Growing tomatoes under field conditions is the cheapest option for most smallholder farmers due to the low resource requirements. Farmers rely on the rainfall pattern with supplementary watering particularly during the dry season. The crops cultivated this way are exposed to the diverse environmental conditions that may prevail in the area [17]. Intensive crop management such as pruning and staking is always difficult under these conditions. Due to harsh environmental conditions in most parts of the tropics, most tomato growers prefer to grow tomato under controlled environments. The main objective of such operations is to attain the full potential of the crop in terms of yield and nutrient content. Growing tomatoes under controlled environments facilitates improved management such as pruning and staking that could improve the yield of tomatoes. Studies have shown that high temperatures particularly in the tropics affect the quality and nutrient content particularly lycopene of field-grown tomatoes [18, 19]. However, growing tomatoes under controlled environments requires more resources that increase the cost of production and make it difficult for smallholder farmers to engage in it.

5. Field conditions

Tomato is mostly cultivated in moderate climates around the world but can thrive well in a wide range of climatic conditions. The vegetative and reproductive processes of the tomato are adversely affected by high temperature stress, resulting in a reduction in fruit quality and yield [20]. In temperate regions, the crop does well within daily average temperature range of 18°C

and high of 25°C, while the warm season temperatures average low of 26°C and a high of 32°C. Significantly higher or lower temperatures can have negative effects on fruit set and quality. Studies have shown that temperatures above 32°C for more than 3 hours a day can induce abortion of flowers resulting in low fruit yield [21]. In Ghana and most parts of West Africa, it is cultivated in the open field under field conditions, or in controlled environments such as greenhouse. The productivity of the tomato crop depends on the yield potential of the genotype, the soil as well as agronomic and management practices that are carried out. Tomatoes can be produced on a wide range of soils varying from deep, medium textured sandy loam or loamy, fertile, well-drained soils [22]. The site for growing tomatoes should be carefully selected based on the topography, soil type, soil structure, and soil management and the cropping history of the land (fields previously cropped to solanaceous crops should be avoided). Tomato plants depend on the soil for adequate nutrient and water supply as well as anchorage for physical support. For this reason, land preparation should be adequately done to ensure proper plant establishment and to provide the best soil structure for root growth and development. Tomatoes require soils that are rich in nutrients but most soils in Sub-Saharan Africa are low in nutrients due to continuous intensive cultivation without adequate application of soil amendment measure [23, 24]. The potential of organic and inorganic fertilizers can provide the needed solution for intensive tomato cultivation, but this is limited due to scarcity, cost implications, and problems with high acidity associated with over application of such fertilizers [25]. The application of green manure can also provide a viable alternative for maintaining soil fertility but its use is limited among tomato farmers in Ghana [26].

5.1. Controlled environments

In most parts of the tropics, tomato production is weather dependent and highly seasonal. This had led to fluctuations in glut during peak harvest and scarcity during the unfavorable periods of the season. This scenario often affects the pricing and revenue of the growers as well as consumer satisfaction [27]. The use of controlled environment in tomato cultivation can address the challenges faced by tomato farmers to provide suitable environment for growing tomatoes during the off-season and meet consumer demands. Several controlled environments are used in tomatoes cultivation.

6. Screenhouse/greenhouse

Greenhouse tomato production utilizes techniques that are not used in the open field or other intensive cropping systems. In the greenhouse, water, carbon dioxide, artificial lighting, soil-less growth medium such as hydroponics and heating systems are provided to simulate the growing conditions that occur in the open field [28]. Most greenhouses are used in association with drip irrigation systems that regulate and save the amount of water that will be required to produce the optimum yield. In some cases, only 25% of the water required in the open field is used to produce the same quantity in the greenhouse [29]. This is very useful in areas that are faced with extreme temperatures and water scarcity [28] and will be crucial in crop production

especially with the imminent shortage of water that will be associated with climate change and variability. The use of greenhouse technology in tomato cultivation combines market-driven quality parameters with the production system that enhances the quality and quantity of the final product. Provision of the necessary intensive plant care is possible without the excessive use of chemical pest management. This is because better protection is achieved through the use of integrated pest management strategies that are more effective under controlled environments than in open field [30]. Cultivation of tomato under this system ensures that the high profit margins due to premium prices offered the good-quality products obtained because in addition to higher yield, the production is also free from dust, insect, disease, and pest [31]. Greenhouse-grown round and cluster tomatoes were found to contain higher levels of lycopene than field-grown tomatoes. However, the opposite was the case with cherry tomatoes which recorded lower levels of lycopene under greenhouse conditions compared with open-field cherry tomatoes. These reports suggested the presence of genotype by environment interaction effect [18]. Therefore, careful varietal selection should be done when utilizing the greenhouse technology in tomato cultivation. Besides careful varietal selection, energy consumption is also one area that needs to be considered critically when deciding the type of technology to be used for maximum profit [32].

6.1. High tunnel

Tomatoes are well adapted to the growing conditions within a high tunnel. A high tunnel often called *hoophouse* is a solar-heated, manually controlled vented structure cold frame that is covered with plastic (single or double layer) for cultivation of many horticultural crops with the purpose of lengthening the growing season. Though similar in appearance to some greenhouses, they lack some features of greenhouses such as electricity for temperature and humidity regulation, and thus require no electrical connections for ventilation and supplemental heat [33–35]. However, most high tunnels have roll-up sidewalls and detachable end walls for temperature and humidity management. High tunnels can significantly increase the average daily temperature and protect the crop from wind, rain, insects, and diseases. Crops are grown directly in the soil using raised beds or mulch [36, 37]. Since high tunnels exclude natural rainfall so water must be applied through irrigation. Drip irrigation significantly improves the marketable yield and overall quality and is the best form of irrigation for tomatoes grown under high tunnels. It ensures uniform application of water to help reduce fruit cracking and other physiological problems such as blossom end rot. In most intensive cultivation using the high tunnel technology, both water and nutrients are supplied to the crops during the growing season with drip irrigation [38]. When tomatoes are cultivated in high tunnels they can be trained to grow vertically by the use of trellis or staking (**Figure 1**).

6.2. Hydroponics

Hydroponic tomatoes are grown in a nutrient solution rather than soil. The plants are typically placed in a nonsoil material known as substrata that can support their roots and hold the nutrients. In some cases, hydroponic system utilizes absorbent substrata such as coconut fiber, perlite, rock wool, vermicompost, and their combinations [39, 40] together with a drip-irrigation



Figure 1. Interior and exterior features of high tunnels for controlled vegetable cultivation.

system which supplies water at low tension and high frequency to create optimum environment for growth of the vegetable [41, 42]. By avoiding soil medium, the use of hydroponics enables the grower to prevent diseases and soil-borne pests, such as nematodes, that are difficult to control [43]. Tomato production under protected systems such as hydroponics allows cultivation in regions inappropriate for conventional agriculture by efficiently using natural resources particularly water and soil [44]. Hydroponic systems provide regulation of harvesting, avoiding crop rotation, better fruit quality, better crop handling, and better control over nutritional needs and environmental conditions. Growing tomatoes under hydroponic system allows the grower to raise them under a controlled environment with less chance of disease, faster growth, and greater fruit yield. This offers several advantages in terms of the quantity and quality of products obtained per unit land area over cultivation in soil [45].

However, hydroponic gardening is labor-intensive and requires skilled training for efficient water and nutrient management under large-scale production. It has been suggested that one of the major problems of using the hydroponics systems for tomato cultivation is its requirement for highly specialized technical support in order to properly replenish the nutrient solution in all the growing phases of the crop [43] (Figure 2).

6.3. Irrigation

The tomato plant like most vegetable crops requires a lot of water for optimum growth and development. Moisture stress causes abortion of flowers and young fruits, and young fruit, sun scalding, and dry rot of fruit. Water is required at most critical stages of growth of the

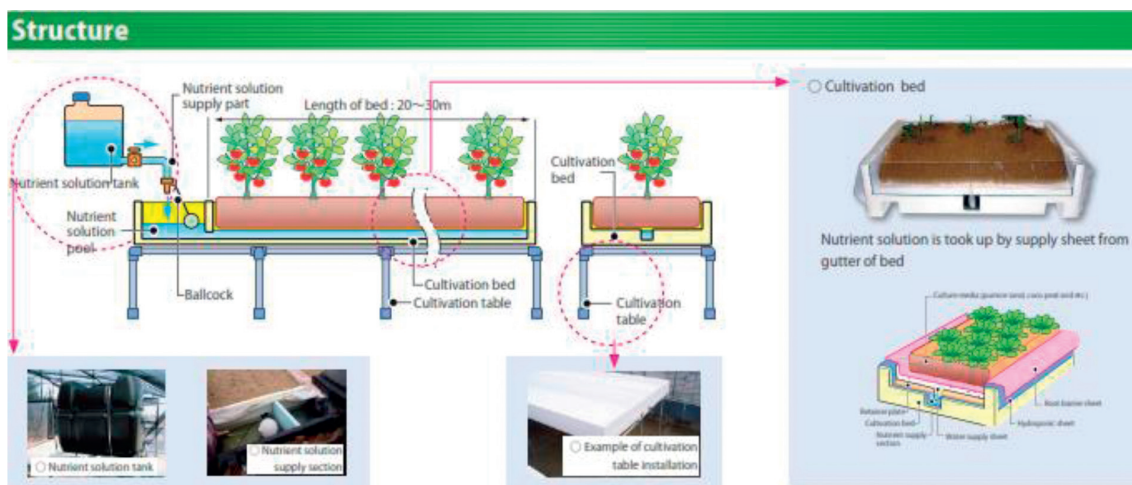


Figure 2. Dutch bucket hydroponic system for cultivating tomatoes (https://www.google.com.gh/search?tbm = isch&sa = 1&q = hydroponics+tomatoes&oq = hydroponics+tomatoes&gs_l = psy-ab.3..0j0i5i30k1j0i24k116.202616.205468.0.206233.9.9.0.0.0.384.1735.2-5j1.6.0....0...1.1.64.Psy-ab..3.6.1732...0i67k1.0.HQe-PNKGi6I#imgrc = gjqgs0WVVSaQvuM).

tomato plant particularly at transplanting, flowering, and fruit development. Adequate supply of water is very essential for attaining the full potential of tomato plants under cultivation [31, 32]. However, agricultural activities in most parts of the tropics are mostly rainfed resulting in short supply of water for farming activities during the dry season. Rainfall amounts are often erratic even during the main growing season resulting in poor crop performance especially in areas where tomatoes are grown in soils with low water holding capacity. The use of irrigation schemes provides the needed water required for crop production. This makes supplemental irrigation essential for commercial tomato production to sustain consistent yields of high-quality tomatoes during the off-season to meet demand of consumers. Studies have shown that irrigation increases annual tomato yields by an average of at least 60% over dryland production [32, 33]. The quality of tomatoes cultivated under irrigation has also been found to be better than nonirrigated fields [20].

7. Types of irrigation in tomato cultivation

7.1. Sprinkler irrigation

These systems include center pivot, linear move, traveling gun, permanent set, and portable aluminum pipe with sprinklers that supply the irrigation water in sprays to the crops. The idea is to mimic the natural rain drops. Sprinkler systems used in tomato production are normally adjusted to deliver at least an inch of water every 4 days. The system is also designed to supply the water in such a way that runoff is prevented [41]. The type of soil is also considered in adjusting the speed of the sprinkler irrigation system. Whereas faster speed (3 inches per hour) is preferred in sandy soils, slower speed is preferred in loamy soils (1 inch per hour). High level of application uniformity is essential every plant is covered to ensure uniform growth and development throughout the field [42].

7.2. Drip irrigation

Drip irrigation has become the standard practice for tomato production. Although it can be used with or without plastic mulch, its use is highly recommended with plastic mulch culture. One of the major advantages of drip irrigation is its water use efficiency. When used in conjunction with plastic mulch, the tubing can be installed at the same time the plastic mulch is laid. In drip irrigation system, water is delivered to each plant usually done with tubes and emitters that carry water from main lines to the base of each plant. In some cases, fertilizer is included in the irrigation water in a system appropriately called "fertigation" [41, 46]. The important thing to note is that water is supplied in such a way that the plants do not wilt. Studies have also shown significant yield increases with drip irrigation and plastic mulch when compared with sprinkler-irrigated tomatoes. The most dramatic yields have been attained by using drip irrigation and plastic mulch, and supplementing nutrients by injecting fertilizers into the drip system. This observation is due to judicious utilization of the water and nutrient resources that are supplied to each plant which is not the case with sprinkler irrigation system. The incidences of weeds also less of a problem, since only the rows are watered and

the middles remain dry. Another advantage of drip irrigation is obtained when used in within a high tunnel which is equipped with the ability to inject water-soluble nutrients through the drip lines as the plant needs them.

8. Genotype × environment 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 [47]. Data generated from such trials are important for (i) accurate estimation and prediction of yield based on limited experimental data; (ii) determining yield stability and the pattern of genotypes response across environments; and (iii) providing reliable guidance for selecting the best genotypes or agronomic treatments for planting in future years and at new areas [48]. However, the performances or ranking of the genotypes in such experiments are usually not the same in the different environments. This is because of interactions between the genotypes and the environments [49, 50]. This type of interaction is known as genotype × environment interaction (GEI), and may complicate the selection and recommendation of genotypes evaluated in diverse environments [51, 52]. The importance of GEI in genotype evaluation and breeding programs has been demonstrated in almost all major crops [53–57]. The GEI 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 [57].

Genotype × environment interactions can be classified into three broad types (**Figure 3**) (i) “no” GEI, (ii) non-crossover interaction, and (iii) crossover interaction [58]. The number of environments (E) and the number of genotypes (G) determine the number of GEI possible and that, the higher the number of environments and genotypes the greater the number of possible G × 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 [59, 60].

9. No G × E interaction

When there is no GEI, the effects of each of the risk factors are similar across the levels of the other risk factors. A “no” GEI occurs when one genotype (G1) constantly performs better than the other genotype (G2) by approximately the same amount across both environments. **Figure 3A, B** shows that G1 and G2 perform similarly in two environments, because their responses are parallel and stable. The variations in trait expression across a range of environments for the two genotypes are therefore additive. Moreover, the intergenotypic variance

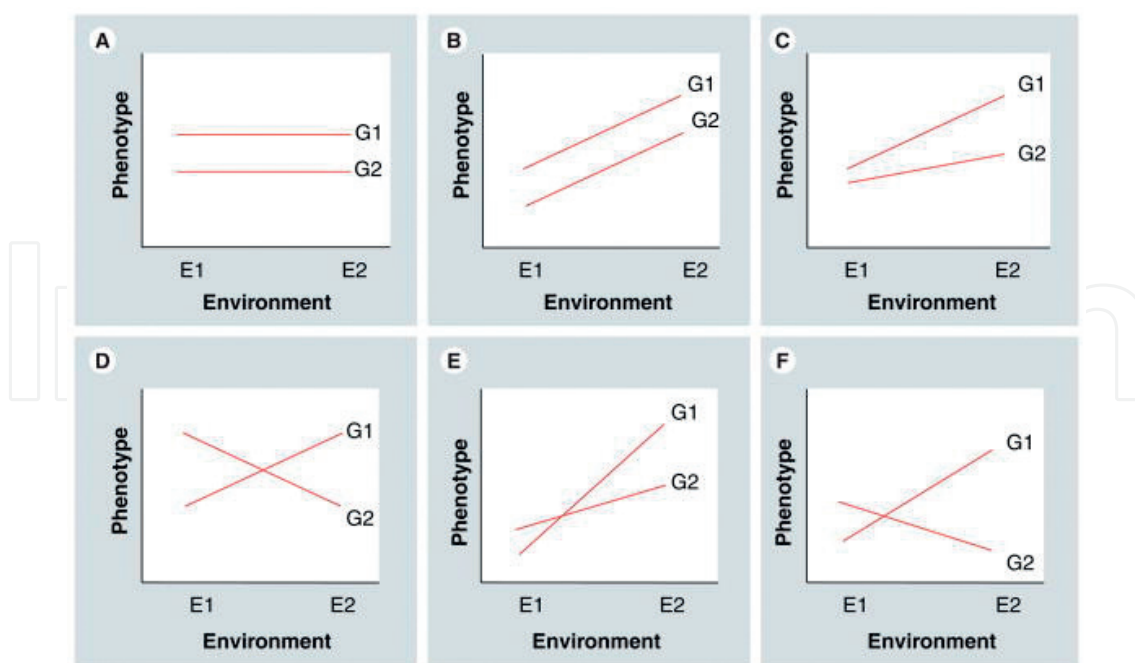


Figure 3. Graphical representation of the “no” interaction, non-crossover interaction, and crossover interaction types of genotype-environment interactions (Source: [58]).

remains unchanged in the two environments and the direction of environmental modification of genotypes is the same. In **Figure 3A**, there is a main effect of G, and in **Figure 3B**, there is a main effect of environment [58].

10. Non-crossover $G \times E$ interaction

Figure 3C signifies a non-crossover type of GEI. Unlike in **Figures 3A** and **3B**, the difference in performance is not similar across the environments. The G1 and G2 respond differently to the two environments but their ranks remain unchanged. The response of the two genotypes under different environments is therefore not additive, and the magnitude of intergenotypic difference increases. Moreover, the environmental modifications of the two genotypes are in the same direction [58].

11. Crossover $G \times E$ interaction

The different and inconsistent response of genotypes to diverse environments is regarded as crossover GEI, when the ranks of genotypes vary from one environment to another [1]. Crossover interaction suggests that no genotype is superior in multiple environments [61]. **Figure 3D** illustrates a crossover type of GEI where the direction of environmental modification of genotypes, G1 and G2 is opposite: the performance of G1 increases and that of G2 decreases. The genotypic ranks change between the two environments, but the magnitude of

intergenotypic variance remains unchanged. **Figure 3E** is also a representative of a crossover interaction as the genotypes change ranks between the two environments. There is also a change in magnitude of intergenotypic variance. Moreover, the difference between genotypes G1 and G2 in environment E1 is smaller than that in E2, and the direction of environmental modification of the two genotypes is the same. The illustration in **Figure 3F** is a crossover interaction with the environmental modification in opposite direction [58].

12. Multilocation trial for tomato production

Multilocation trials are conducted to evaluate yield stability performance of genetic materials under varying environmental conditions [55]. The relative performance of genotypes for quantitative characteristics, such as yield and other characteristics, influences yield to vary from an environment to another. To develop a genotype with high yielding ability and consistent performance, high attention should be given to the importance of stable performance for the genotypes under different environments and their interactions. This enables the breeding of better crop varieties that have buffered and can give stable and consistent performance across different environments and seasons [59]. To attain this, feat genotypes are evaluated in multienvironment trials (METs) by testing their performance across environments and selecting the best genotypes in specific environments. The main objective is to eliminate genotype by environment interaction results from differences in the sensitivities of genotypes to the conditions in the target environment [62]. This leads to inconsistent performances of genotypes across environments and limits the efficiency of selection of superior genotypes [56].

13. Tools/methods for genotype × environment interaction analysis

Analysis of GEI is important to obtain information on the performance of genotypes in terms of adaptability and stability. Analysis of variance is performed across environments in order to identify the presence of GEI in multilocation trials. When the GEI variance is found to be significant, then one of the various methods for measuring the stability of genotypes can be used to identify the most stable genotype(s). Several statistical methods have been proposed for analysis and interpretation of GEI [63–66]. The joint regression analysis [67–69] method has been widely used; nonetheless, several limitations of the method have been stated [70, 71]. For example, see [48]. The PCA method has the ability to overcome the limitations associated with the linear regression method by giving more than one statistic, that is, the scores on the principal component axes, to describe the response of a genotype. Another method which has been proposed for analysis of GEI is the cluster analysis which is a numerical classification technique that defines groups of clusters of individuals [48, 72]. Currently, the additive main effects and multiplicative interaction (AMMI) model [64, 71] and genotype main effect plus genotype × environment interaction (GGE) biplot methodology [66] are the two most powerful statistical tools used by many researchers for the analysis of multilocal trial data. The AMMI model combines the analysis of variance for the genotype and environment main

effects with principal component analysis of the genotype \times environment interaction. It also provides a better prediction assessment and a valuable approach for understanding GEI and obtaining better yield estimates. The interaction is described in the form of a biplot display, where PCA scores are plotted against each other and provides visual inspection and interpretation of the GEI components. Integrating biplot display and genotypic stability statistics enable genotypes to be grouped based on similarity of performance across diverse environments. Similarly, the GGE biplot analysis enables visual (graphical) presentation of interaction estimate. This method also combines analysis of variance and PCA by partitioning together sums of squares of genotypes and sums of squares of GEI (which are relevant in genotype evaluation) using PCA method. The biplot technique is used for the presentation and estimation of genotypes in different environments [73]. The GGE biplot shows the first two principal components (PC1 and PC2) which are obtained by decomposition of singular values of multilocation trials yield data. GGE biplot analysis enables the identification of the genotypes with the highest yields in different environments, comparison of their performances in different environments, identification of ideal genotype, as well as mega-environments (model of regional distribution or target environment) [74, 75].

Several researchers have compared the efficiency of AMMI and GGE biplot for analyzing GEI. According to Yan and others, the major disadvantage of the AMMI model is that it is insensitive to the most important part of the crossover GEI [75]. Moreover, the AMMI model does not offer any advantage to the breeder for genotypic and site evaluation when analyzing METs data because there is no clear biological separation between the two terms, genotype and GEI. However, the GGE biplot is a powerful statistical model that takes care of some of the disadvantages of AMMI. The method is an effective statistical tool for identifying the best performing cultivar in a given environment and the most suitable environment for each cultivar, comparison of any pair of cultivars in individual environments, the best cultivars for each environment and mega-environment differentiation, average yield and stability of the genotypes, and the discriminating ability and representativeness of the environments [75–77]. Gruneberg and others indicated that AMMI was highly effective for the analysis of MET [78]. Kandus and others also revealed that the AMMI model is the best model for describing the GEI [79]. Stojaković and others [80] and Mitrovic and others [81] found that both models provided similar results. However, contrary to these reports, [75, 82, 83] concluded in their comparison of both models that the GGE biplot was superior to the AMMI biplot in mega-environment analysis and genotype evaluation.

14. Prospects and problems of $G \times E$

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. $G \times E$ interaction 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 [53, 76]. Though tomatoes do well in both tropical and temperate climates, its performance can vary with respect to the environments [18]. Prior to the release of every crop variety, multilocation

trials are conducted to ascertain crop performance in a wide range of environments for adaptability and stability in performance [47].

14.1. Causes of genotype × environment interaction

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 [84]. This is because genotypes exhibit different levels of phenotypic expression under different environmental conditions resulting in crossover performances [85]. Crossover performances by genotypes in different environments result from differential genotypic responses under varying environmental conditions [63, 86]. This results in genotype by environment interaction where one genotype gives its maximum performance in one environment by performing poorly in another environment. In $G \times E$ interaction, the magnitude of the observed genetic variation changes from one environment to another and tends to be larger in better environments than poorer environments [87].

14.2. Problems of genotype × environment interaction effect on selection

The objective of most plant breeders is to develop new varieties that will perform consistently well across multiple environments. However, significant $G \times E$ interaction has been reported for most quantitative traits in tomato particularly for fruit yield and quality traits such as lycopene, total soluble solids, vitamin C, etc. [19, 88]. A tomato variety with improved fruit quality in one environment may not necessarily perform the same in another location due to differential responses to the different environmental conditions prevailing in the different locations. Environmental factors such as soil, moisture, temperature, light intensity, humidity, rainfall, photoperiod, and agronomic practices play important role in the expression of the genes controlling the trait of interest. This results in different phenotypic expression among locations. Genotype × 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. In some cases, the quality of fruits of tomatoes is significantly influenced by genotype by environment interaction. Such interactions confound the selection of the superior cultivars by altering their relative productiveness in different environments. For instance, see [89]. Other studies [90] also reported significant $G \times E$ interaction effect on total sugars among six tomato varieties grown under field and greenhouse conditions. This problem implies that tomato varieties that were developed and selected under field conditions may not perform to its full potential when farmers grow them under controlled environments. Therefore, the extent of $G \times E$ interactions effect for most traits of economic importance needs to be taken into account during the selection process in order to obtain crop varieties that will give consistent performance across environments and seasons.

14.3. Elimination of genotype × environment interaction

Breeding of crops involves different attributes of the genetic materials that are subject to variation in environmental conditions [91]. In some cases, direct selection is slow due to low heritability, polygenic control, epistasis, and significant $G \times E$ interaction on the trait of interest

[92]. To mitigate the confounding effect of $G \times E$ interaction on selection efficiency, plant breeders have devised strategies to ensure progress in selection efficacy. For this reason, genotypes are tested in diverse environments to assess their adaptability and stability [85]. After this sound, analyses are carried out using the appropriate software to assess the extent of $G \times E$ interaction effect. Genotypes whose $G \times E$ effects are not significant are considered to be stable and therefore selected [62].

Stability analysis is performed to estimate the performance of genotypes as linear function of the level of productivity in each environment [93]. Eberhart and Russell suggested joint regression analysis to estimate the average performance of a genotype in different environments relative to the mean performance of all genotypes in the same environment [68]. The use of multiplicative models which include the additive main effect and multiplicative interaction (AMMI) model has also been used to assess the stability of other crops [94, 95]. The AMMI model allows fitting of the sum of several multiplicative terms rather than only one multiplicative term in dissecting the performance of genotypes in different environments [93]. Yan also suggested the use of the genotype and genotype \times environment interaction (GGE) biplot to graphically visualize genotypic performance across several environments [96]. The use of these strategies will enable the breeder to make informed decisions in where to place which variety based on their adaptability for optimum performance.

15. Conclusion

The pounding prominence of tomato as a vegetable is reflected by large volume of research on almost all aspects of the crop. In every crop improvement program, promising genotypes are tested for their performance for some years at a number of sites, to identify genotypes which possess the dual qualities of high-yield sustainability to adverse changes in environment condition. This interplay refers to genotype by environment interaction. A genotype \times environment interaction is a change in the relative performance of a character of two or more genotypes measured in two or more environments. Its origin is linked to two concepts: biometric and developmental interaction. Interactions may therefore involve changes in order for genotypes between environments and changes in the absolute and relative magnitude of the genetic, environmental, and phenotypic variances between environments. These can further be classified as no GEI, non-crossover interaction, and crossover interaction. Complex quantitative traits, such as yield, with multiple contributing traits are highly influenced by environment interaction effects. Tomato production, though weather dependent and highly seasonal, can be grown under both field and greenhouse conditions (controlled environment). Researchers perform multilocal trials to evaluate new or improved genotypes across multiple environments (locations and years), before they are promoted for release and commercialization. This organized approach helps increase yield stability of new crop varieties in stress-prone environments. To obtain information on the performance of the genotypes in terms of adaptability and stability, an analysis of the GEI is paramount. Even though several statistical methods have been proposed for analysis and interpretation of GEI, the joint regression analysis method has been widely used; nonetheless, it has numerous limitations. Many other researchers have also found AMMI and GGE biplot efficient for analyzing GEI. A major

problem of GEI is that its effect thwarts the selection of suitable varieties by breeders because elite varieties developed for one location may not perform the same in different locations. In some cases, the quality of fruits of tomatoes is significantly influenced by genotype by environment interaction. Such interactions confuse the selection of the superior cultivars by altering their relative productiveness in different environments. Though tomatoes do well in both tropical and temperate climates, its performance can vary with respect to the environments.

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