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Genotype by Environment Interactions: Effects on Plant Growth and Productivity

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Abstract: In agricultural experimentation, a large number of genotypes are normally tested over a wide range of environments (locations, years, growing seasons, etc.). Multi-environmental trials are essential to study genotype by environment interaction (GEI) for effective variety selection and cultivar recommendation in breeding programs. Matching variety selection with its production environment is often challenged by the occurrence of significant GEI in the variety development process. GEI is one of the main complications in the selection of broadly adapted varieties in most breeding programs. In the absence of GEI, the superior genotype in one environment may be regarded as the superior genotype in all, whereas the presence of the GEI confirms particular genotypes being superior in particular environments. Where environmental differences are great, it may be expected that the interaction of genotypes with the environment will also be great. 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 GEI to know the magnitude of the interactions in the selection of genotypes across several environments besides calculating the average performance of the genotypes under evaluation. Crop breeders/agronomists have been striving to develop genotypes with superior grain yield, quality and other desirable characteristics over a wide range of environmental conditions. Numerous research studies have shown that a proper understanding of the environmental and genetic factors causing the interaction as well as an assessment of their importance in the relevant genotype by environment system could have a large impact on plant breeding.

Key words: Environment · Genotype · Genotype Environment Interaction · Stability · Yield

INTRODUCTION

Genotype–environment interaction (GEI) is an age-old, universal issue that relates to all living organisms. The term genotype means a cultivar or variety and environment it relates to the set of abiotic, biotic and management conditions in an individual trial carried out at a given location and year. The measured yield of each cultivar in each test environment is a measure of an environment's main effect, a genotype main effect and the GEI [1, 2]. The term GEI commonly refers to yield variation that cannot be explained by genotypes or the environment alone [3]. GEI refers to the deviation in the performance of any attributes of genotypes within the various growing environments. Genotypes and environments interact to produce an array of phenotypes. GEI can be defined as the difference between the phenotypic value and the value expected from the corresponding genotypic and environmental values [4, 5]. The presence of GEI complicates the varietal selection process as it reduces the usefulness of genotypes by confounding their yield performance by minimizing the association between genotypic and phenotypic values [6]. When genotypes performances are tested at several environments, the rankings usually differ as a specified difference in the environment may produce a different effect on specific genotypes. In highly diverse environments, there would likely be GEI is expected. Consequently, it is not only average performance that is important in the selection of superior genotypes but also the magnitude of the interaction is equally important [7, 8]. Hence, GEI must be either exploited by selecting a superior genotype for each specific target environment or avoided by selecting a widely adapted and stable genotype across environments [9].

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A GEI is extremely important in the development and evaluation of plant varieties because it reduces the genotypic stability values under diverse environments [10]. Developing crop cultivars that perform well across a wide range of environmental conditions has been a major challenge to plant breeders [11]. The plant breeder desires stable genotypes with good performance across all environmental situations. Understanding the knowledge of cultivar performance and yield adaptation in diverse agro-ecological zones is very important for cultivar selection and improvement. A genotype grown in different environments will frequently show significant fluctuations in yield performance [12]. Under various heterogeneous environments, allocating a variety that can successfully be adapted to a certain location or across locations is difficult due to the interaction effects of genotypes with the environment. To solve this problem, experimental research needs to be carried out in multi-environment variety trials to identify and analyze the major factors that are responsible for genotype adaptation [13]. In multi-environment experiments, the influence of the environment is attached to the expression of complex characteristics and reveals a high influence on the environment. The change in the relative behavior of the genotype in different environments is due to the differential response of genotypes to different growing conditions [14]. The GEI makes it difficult to select genotypes that produce high yield and that are more stable and it reduces the selection progress [15]. A cultivar to be successful, it must perform well across the range of environments to which it is grown. The presence of GEI reduces the correlation between phenotype and genotype and makes it difficult to judge the genetic potential of a genotype [16].

Because of the difference in cultivar ranking from place to place due to GEI, it is necessary to subdivide growing regions into several relatively homogenous mega-environments. It is possible to develop genotypes with low GEI via sub-division of the heterogeneous area into smaller, more homogeneous sub-regions; and by selecting genotypes with better stability across a wide range of environments [17]. Another study also indicated that GEI effects reduced by stratifying environments and by selecting adaptable genotypes for each mega-environment or broader region [18]. A mega-environment is defined as a portion of a crop species growing region with fairly homogeneous environments that cause similar genotypes to perform best. Such classification will enable breeders to breed and target adapted genotypes for each mega-environment [19]. Multi-environment evaluation of genotypes provides useful information for this broader or specific recommendation. The GEI may be reduced using specific cultivars for each environment or using cultivars with wide adaptability and good stability or by stratifying the region under study in mega-environments with similar environmental characteristics, within which the interaction becomes small [20]. Mega-environments are generally identified through the analysis of multiple-environment trial data for a diverse set of genotypes. The purpose of mega-environment analysis is to understand the GEI patterns within a target region to explore the feasibility of dividing the target region into meaningful mega-environments that permits the GEI to be exploited to maximize the response to selection within mega- environments and increase the productivity of the target region [21]. It is, therefore, essential that genotypes are identified based on a detailed understanding of their GEI, so that environment-specific recommendations could be made. Therefore, this review paper was summarized to investigate the effects of genotypes by environment interactions on plant growth and productivity.

Importance of GEI in Breeding: GEI presents many challenges for breeders and has significant implications in both applied plant and animal breeding programs. The breeder is faced with developing separate populations for each site type where genotypic rankings drastically change and/or is faced with selecting genotypes that generally perform well across many sites [22]. Gains are expected to be greater with the first approach, but costs would also likely be higher; the second approach, while less expensive, yields smaller gains. Denis and Gower [23] suggested that plant breeders should consider GEI to avoid missing a variety that performed, on average, poorly but did well when grown in specific environments or selecting a variety that, on average, performed well but did poorly when grown in a particular environment. To be able to understand GEI and utilize it effectively in breeding programs, information is needed on the factors responsible for the differential response of genotypes to variable environments. A factor may be present at optimal, suboptimal or super optimal levels. When present at a level other than optimal, it represents stress. According to Baker [4], differences in the rate of increase in the response of genotypes at suboptimal levels would reflect differences in efficiency and differences in the rate of decrease at super optimal levels would reflect differences in tolerance. Without the presence of stresses, genotype attributes, such as efficiency and tolerance, cannot be identified and investigated.

Agricultural production has kept pace with the world's population growth mainly because of the innovative ideas and efforts of agricultural researchers. The world population is increasing at an alarming rate. The key to doubling agricultural production is increased efficiency in the utilization of resources and this includes a better understanding of GEI and ways of exploiting it. The importance of GEI can be seen from the relative contributions of new cultivars and improved management to yield increases from direct comparisons of yields of old and new varieties in a single trial [24]. Genetic improvements have been estimated to account for about 50% of the total gains in yield per unit area for major crops during the past 50–60 years [24-26]. The remainder of the yield gain is attributable to improved management and cultural practices. Barley yield data from the UK (1946–1977: mean yield for 1946 = 2.3 t ha^{-1} and 1977 = 3.9 t ha^{-1}) indicated that the environmental contribution was 10–30% and the genetic contribution 30–60%; the remainder 25–45% of the yield gain was attributed to GEI [25]. For wheat for the same period (1946–1977: mean yield for 1946 = 2.4 t ha^{-1} and 1977 = 4.7 t ha^{-1}), yield gain was attributed as follows: 40– 60% to the environment, 20–40% to the genotype and 15–25% to GEI [25]. The GEI confounds precise partitioning of the contributions of improved cultivars and improved management and cultural practices to yield [24]. Thus, the combined contributions of genotype and G x E effects can be substantial (40–60% wheat and 70–90% in barley) for yield improvement.

GEI has an impact on all stages of a breeding program and has enormous implications for the allocation of resources that are used for the cultivation of crops. A large GEI could mean the establishment of two full-fledged breeding stations in a region, instead of one, thus demanding increased input resources such as manpower, land and money for crop production. Heritability of a trait plays a key role in determining genetic advance from the selection. As a component of the total phenotypic variance (the denominator in any heritability equation), GEI affects heritability negatively. The larger the GEI component, the smaller the heritability estimate; thus, progress from selection would be limited. A large GEI reflects the need for testing cultivars in multiple environments (locations and/or years) to obtain reliable results. If the weather patterns and/or management practices differ in target areas, testing must be done at several sites that are representative of the target areas. Kang [27] discussed the disadvantages of discarding genotypes evaluated in only one environment in the early stages of a breeding program. The discarded genotypes might have the potential to do well in their niche environments' (location or year). Thus, some potentially useful genes could be 'lost' due to limited testing. An example from six-row barley illustrates this point well. A total of 288 barley lines were evaluated in the Maghreb countries and the International Center for Agricultural Research in Dry Areas (ICARDA)'s yield trials at three locations [28]. Of the 103 lines selected at ICARDA and 154 lines at the Magreb, only 49 were selected at both locations.

Performance evaluation is the second component of a breeding program. Testing done in one environment provides only limited information. Multi-environment testing provides additional useful information, e.g. a GEI component can be estimated. Besides, multi-environment testing yields better estimates of variance components and heritability. Therefore, GEI need not be perceived only as a problem. As the magnitude of a significant interaction between two factors increases, the usefulness and reliability of the main effects are correspondingly decreased. Since GEI reduces the correlation between phenotypic and genotypic values, the difficulty in identifying truly superior genotypes across environments is magnified. The cost of cultivar evaluation increases as additional testing is carried out. However, with additional test environments, a breeder/agronomist can identify cultivars with specific adaptation as well as those with wide adaptation, which will not be possible from testing in a single environment. Broad adaptation provides stability against the variability inherent in an ecosystem, but specific adaptations may provide a significant yield advantage in particular environments [29]. Multi-environment testing makes it possible to identify cultivars that perform consistently from year to year (small temporal variability) and those that perform consistently from location to location (small spatial variability). Temporal stability is desired by and beneficial to growers, whereas spatial stability is beneficial to seed companies and breeders. The stability of performance can be determined via stability statistics [30-32]. Thus, GEI is a phenomenon that is very important and is of significance to plant breeders, agronomists and farmers all over the world.

GEI is the change in a cultivar's relative performance over environments, which results from the differential response of the cultivar to various edaphic, climatic and biotic factors [33]. GEI occurs in two ways. Firstly the difference between genotypes vary without alteration in their rank i.e. GEI is present because one cultivar yields more than another cultivar in all the environments and secondly the ranking between cultivars changes across environments i.e. one cultivar will be more productive in one environment, while the other cultivar is more productive in another environment. Studying of GEI is very important to plant breeders because this interaction can limit the progress in the selection process and since it is a basic cause of differences between genotypes for yield stability. Understanding the cause of GEI is important to help in selecting varieties with the best adaptation and that can give stable yields [34]. Variation of cultivars yield performance in different environments may be a contributing factor to productivity due to large GEI [35]. Breeding materials can be selected and assessed based on their different responses to the environments. The GEI poses a serious problem in breeding programs because it is a factor, which can influence any stage of the program, like identifying appropriate sources or parent material. But it can also play a role in the expression of quantitative traits. Variation due to genotype or GEI is a measure of how cultivars either respond similarly across the environment or differently according to different environments.

Factors Affecting GEI: Climatic factors affecting GEI:Water plays a vital role in the growth, yield and nutrient uptake of plants. Insufficient water vigorously affects the germination of the seed, cell division, tillering and nutrient uptake of the plants. Nutrients from the soil reach the surface of a root by mass flow and diffusion processes. Mass flow and diffusion processes are positively correlated with the moisture content of the soil. Movement of nutrients thought the plant body is also associated with soil water content. Application of water without proper planning results not only the wastage of water but also hamper crop growth and yield. The effect of moisture stress on growth and yield attributes of different varieties was observed. In sorghum, the higher values of growth and yield attributes were observed in normal treatment than drought treatment (Fig. 1). The interaction effect of moisture stress on growth and yield attributes of sorghum varieties was statistically significant [36]. Drought is one of the major abiotic stresses in agriculture worldwide, limiting crop productivity [37]. Generally, drought stress reduces growth [38, 39] and yield of various crops [40]. Also reduce the nutrient uptake in plants [41]. Generally, low water availability results in reduced total nutrient uptake and frequently reduces the levels of mineral nutrients in crop plants [41, 42]. It is well evident that drought-stressed plants exhibit various physiological, biochemical and molecular changes to thrive under water-limited conditions [43].

Moisture stress is one of the causes of GEI for yield for various crops [44, 45]. Several research findings have discussed the differential genotypic response to post-anthesis moisture stress in wheat [44, 46, 47]. Wells and Dubetz [48], working with barley, showed a similar response to drought at the heading stage, which resulted primarily from differences in kernel size. Differential genotypic response to post-anthesis stress could thus reflect differences in the ability to utilize reserves as first highlighted by Hunt [49] and elaborated on by Blum *et al.* [50]. Differential response to pre-anthesis stress, when associated with kernel weight rather than kernel number, could also reflect reserve accumulation and utilization differences. Chickpea can show different phonological reactions or responses to climate conditions. This consequently will affect plant growth and productivity differently. Additionally, the location effect contributed to this efficacy. Climate changes will affect early growth and flowering by changing dry matter content, the numbers of fertile and dropped flowers [51]. Rainy conditions in different locations affected the environmental responses of plants. The difference in adaptation abilities of genotypes plus rainy conditions both increased the intensity of their environmental responses. However, plants would have eliminated the negative consequents of climate change when they grew up sufficiently [52]. Some genotypes affected by environmental factors to a lesser extent this showed better growth performance than the others.

GEI is highly significant indicating that genotypes responded differently to normal and stress conditions. However, the variability is greater under rain fed drought conditions as compared to irrigated conditions. A study of variation in wheat yield in 57 countries over a 30-yr period showed that rainfall and its distribution were one of the factors contributing to this diversity [53]. Genotypic differences in yield and its components among genotypes grown under stress conditions could lead to identifying the most tolerant and most sensitive ones [54]. On the other hand, selection for yield under stress conditions is complicated by low heritability and large genotype by environment interactions [55]. The most widely used criteria for selecting high yield performance are mean yield, mean productivity and relative yield performance in stressed and favorable environments [56].

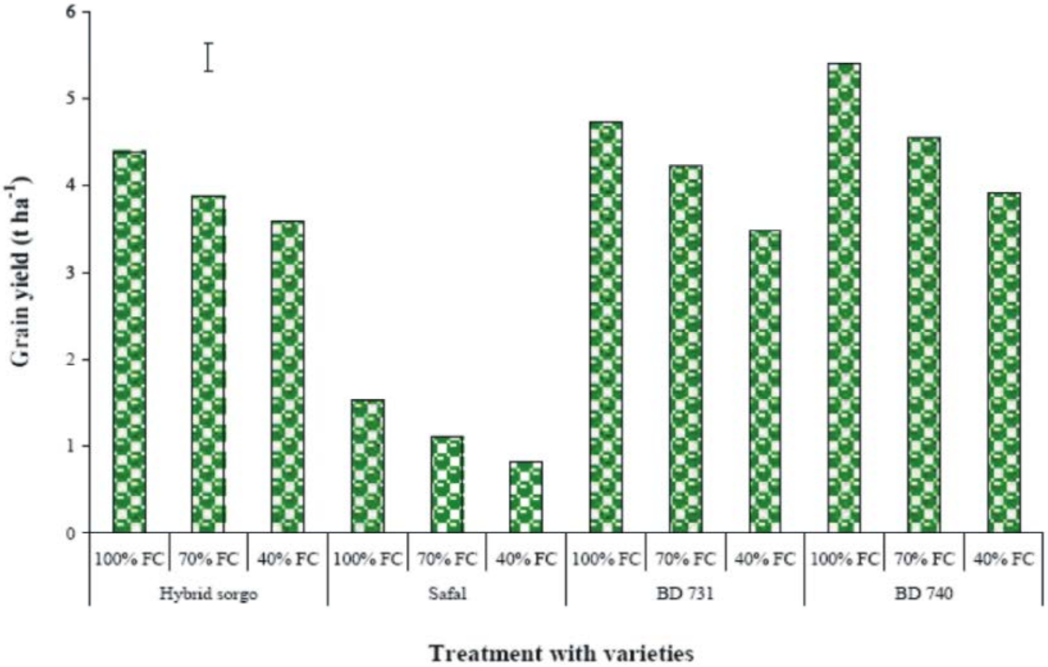

Fig. 1: Interaction effect of moisture stress and varieties on grain yield of Sorghum (vertical bar indicates LSD at a 1% level of probability). Source: [36]

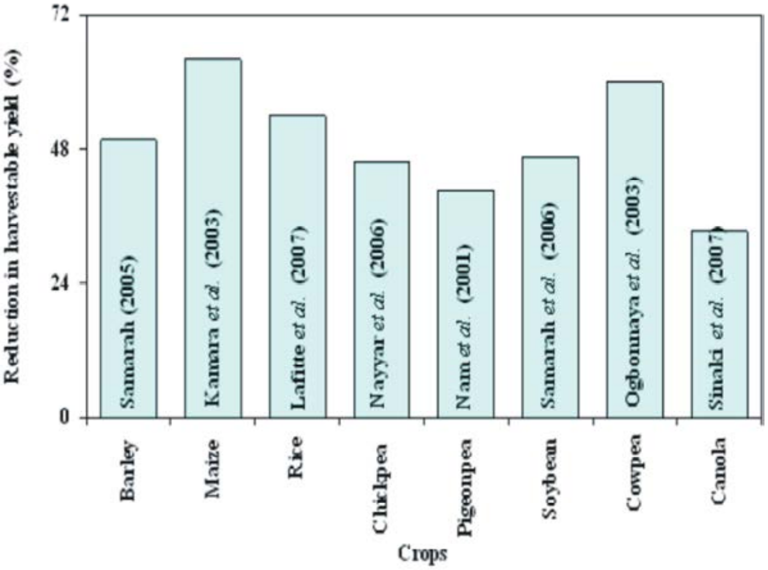

Fig. 2: Loss of harvestable yield in different crop species when the drought stress was applied at the reproductive stage (as indicated in the sources mentioned in the bars). Source: [64]

Severe water stress may result in the arrest of photosynthesis, disturbance of metabolism and finally the death of plants [57]. Water stress inhibits cell enlargement more than cell division. It reduces plant growth by affecting various physiological and biochemical processes, such as photosynthesis, respiration, translocation, ion uptake, carbohydrates and nutrient metabolism and growth promoters [58]. In plants, a better understanding of the morpho-anatomical and physiological basis of changes in water stress resistance could be used to select or create new varieties of crops to obtain better productivity under water stress conditions

[59, 60]. The reactions of plants to water stress differ significantly at various organizational levels depending upon intensity and duration of stress as well as plant species and its stage of growth [61]. Understanding plant responses to drought are of great importance and also a fundamental part of making the crops stress-tolerant [62, 63]. Fetching greater harvestable yield is the ultimate purpose of growing crops. The crop species show great differences for harvestable yield under drought stress (Fig. 2).

Seasonal fluctuations have a potential impact on crop development and grain yield. The variation in temperature requirements and temperature extremes varies widely for different cultivars of the same species, among species and it varies widely for most crops. Kalra *et al.* [65] emphasized the need for studying the response of crops to weather variations for evaluating the impact of seasonal temperature change and estimating yield dependence of temperature rise of crops. Genotypes that perform better in highly stressed environments at one location may perform better at similar locations elsewhere [66]. High yielding genotypes do not perform on par with abiotic stress adapted genotypes when the yield is depressed below a crossover point [67]. Although, approaches other than that based on breeding for yield per se have been proposed [68]. Yield and yield traits continue to be important in measuring the success of a genotype in heat-stressed environments. A genotype with stable and high yield across the environments would be more suitable as a cultivar and also as a donor parent for further breeding in hot environments that vary over the years and within a particular year across locations. The performance of the wheat genotypes was much higher in the normal season than in the late season, which agrees with numerous reports of many researchers on the impact of heat stress on wheat. Rahman *et al.* [69] further stated that in response to a higher temperature, there was a significant reduction in the number of days to booting, heading, flowering and maturity. Singh *et al.* [70] observed that heat stress harmed the growth of wheat. Exposure to higher temperatures can significantly reduce grain yield productivity [71]. In the genotypes of durum wheat, the difference of total grain weight/spike can mostly result in variations in the number of grains/spike but not in the individual grain weight [72]. Moreover, under heat stress, during grain growth, between bread and durum wheat, the differences in the yield/spike might result in the interactions between high temperatures and individual grain weight [72, 73, 74]. Additionally, the highly significant temperature by genotype interactions might also suggest the occurrence of genetic variability too high temperature [72, 73, 75].

Soli Factors Affecting GEI: The variation in soil types and their differential feeding effect on micronutrients are evident for genotype by environment component of variation. The uptake of plant nutrients depends on several factors, such as cultivar, environment, soil fertility and fertilization methods [76-78]. The excess of applied fertilizer or nutrient content in the soil does not produce benefits to plants or may even depress the uptake of nutrients as well as crop growth and yield [79], either concerning nitrogen [80, 81] or phosphorus and potassium [80, 82, 83]. Many researchers have reported that soil variability has a greater impact on crop growth, yield and quality than other production factors [84, 85]. Carr *et al.* [86] reported that grain yield and protein content of a barley cultivar and a wheat cultivar differed across three soils and observed soil fertility by cultivar interactions for test weight and grain protein content. Other workers have reported significant variety by location and variety by year by environmental interactions [84, 86, 87]. Significant soil fertility and cultivar interactions indicate that wheat genotypes react differently to different soil fertility situations. Research output also showed that variations in soil nutrient status can result in grain yield and grain quality differences, often in the same field [85, 86, 88]. Such results show that breeding and cultivar evaluation should place more emphasis on soil fertility and GEI for improved growth, yield and quality.

In analyzing a GEI, an index for each environment (the mean performance of all genotypes in an environment) may be used as a suitable index of its environmental productivity [89]. The performance of each genotype can be plotted against this index. When a nutrient is deficient in the natural soil, natural selection probably leads to the development of plants that store a higher concentration of that nutrient in the seed, for the benefit of succeeding generations [90]. The existence of interaction of genotype by the level of nitrogen (N) fertilization has been shown in maize [91, 92]. At high N input, variation in nitrogen use efficiency (NUE) has been attributed to variation in N uptake capability, whereas, at low N input, variation in NUE is mainly due to differences in N utilization efficiency of the genotypes [93, 92]. N utilization efficiency reflects the ability of the genotype to translate the N taken up into economic yield.

This parameter has been extensively used to compare different species or cultivars at different levels of N fertility [94]. Delogu *et al.* [95] found that barley outperformed wheat in this respect, suggesting a higher ability of barley to generate yield, particularly at low N input. Ideal cultivars would be those that perform well under low soil fertility conditions but also respond well to applied fertilizer [96].

Crop yield improvement response to potassium (K) fertilization on low K testing soils is a fairly uniform response, there can be genotypic variation for this response. This phenomenon has been demonstrated in cotton. While Pettigrew *et al.* [97] did not find any genotypic differences in the lint yield response to K fertilization among the group of eight genotypes used. However, other research findings indicated that some genotypes were more responsive to K fertilization than other genotypes [98-101]. Furthermore, the more potassium responsive genotype in the study by Cassman *et al.* [99] was subsequently shown to produce a more extensive root system than the less K^+ efficient genotype [102]. Therefore, the genotypic differences in K^+ response are probably because more K^+ responsive genotypes were able to take up K^+ at a greater rate or more efficiently because of a bigger root system. Clement-Bailey and Gwathmey [103] also reported that K^+ fertilization was more critical for early maturing cotton varieties rather than later maturing varieties, but Pettigrew [104] did not find the maturity to play a role in the responsiveness of the crop to K^+ fertilization.

Genotypic differences for K^+ uptake and use efficiencies have also been detected in other crops. Maize hybrids were demonstrated to differ in K^+ uptake efficiencies with the more efficient K^+ uptake hybrid was also being the highest yielding [105]. Other research reports indicated that prolific maize hybrids responded more favorably than non-prolific hybrids to high-input cropping systems (including additional K^+ fertilization), primarily by increasing kernel weights and yield [106]. Although a K^+ deficiency tolerant maize hybrid produced more dry matter and an increased number of lateral roots than a K^+ deficiency sensitive hybrid, the sensitive hybrid possessed longer taproots [107]. Genotypic differences among wheat varieties have also been detected in K^+-use efficiency (gram of dry matter per gram K^+) for both grain and stalk production [108]. Damon and Rengel [109] detected wheat genotypic differences in the K^+ efficiency ratio (the ratio of growth at deficient and adequate K supply). Furthermore, a wheat mutant was identified that accumulated more K^+ in the leaf tissue than the wild-type line [110]. Also, soybean varieties have been demonstrated to differ in total K^+ uptake with these total K^+ uptake differences associated with yield potential [111].

The environment and interaction effects are much more than the effects of the genotypes in most variety trials [13, 112]. Micronutrient concentration is affected by a range of factors, including soil type and fertility, soil moisture, environmental factors, crop genotype and interactions among the nutrients [113]. The G × E has been attributed to various micro-environmental conditions, besides soil profile [114]. Although the soil micronutrient status is one of the major factors for kernel micronutrient variations, micro-environmental variations could have profound effects on kernel micro-nutrients; particularly zinc concentration [115]. Rocha *et al.* [116] studied the effect of GEI on the oil content of 28 soybean lines and reported that there were significant genotypes, environments GEI effects. Environment and GEI together captured the largest portion of the total sum of squares (86.8%) in the case of grain yield, indicating the influence of environment and interaction effects in evaluating soybean genotypes for grain yield [117].

Genotypic differences in different soil pH levels have been reported in crops like; pearl millet [118], alfalfa [119] and wheat [120, 21]. In acid soils, Little [121] reported that plant species differ in their aluminum (Al) tolerance; some are inherently more tolerant than others; for example, cassava, cowpea, groundnut, pigeon pea, potato, rice and rye. A substantial genotypic variation in acidity tolerance was found among wheat genotypes, with the root length per plant at pH 3.9 ranging from 66 to greater than 350 mm [122]. The genotypes showed poor agronomic and yield performance as the soil pH decreased from 5.5 to 3.5 indicating that the genotypes are sensitive to acidic soil conditions. An increase in soil acidity was observed to have a deleterious effect on the root growth and the overall growth and development of the soybean genotypes. The genotypes initiated poor root growth at soil pH less than 5.5 suggesting that acid soils inhibit root growth. Kuswantoro *et al.* [123] reported that acid soil effects showed different root growth responses, where the tolerant genotypes had higher root length and susceptible genotypes had suppression on root growth. Fageria [124] observed differential responses in root growth among the rice genotypes to different levels of Al^{3+} while Delhaize *et al.* [125] reported a significant inhibitory effect of Al^{3+} on root growth in wheat genotypes. According to Kochian *et al.* [126], the limiting factors for plant growth in acid soils include the toxic levels of aluminum (Al), manganese and iron (Fe), as well as deficiencies of some essential elements, such as phosphorus (P), nitrogen, potassium (K), calcium (Ca), magnesium and some micronutrients. It is now evident that some plant species can tolerate high salinity [127, 128]. Significant differences in character have also been reported among varieties of different species including wheat [129, 130] and cotton [131, 132]. The differential behavior of plant species may be helpful for the exploitation of these soils by growing fairly tolerant genotypes.

Management Factors Affecting GEI: Development of improved and appropriate agronomic practices (seeding rate, seeding methods, seedbed preparation, fertilizer rate and time of application) would greatly contribute to higher productivity of the crop [133]. There are significant differences in DM production and nutrient uptake among maize genotypes [134]. Different genotypes perform differently owing to their time to maturity and yield, which were the most important factors that influence maize yield [135]. Many researchers studied the performance of different maize genotypes under different planting methods and concluded that maize planted on ridges and raised beds performed well regarding growth and final yield of maize [136-138]; but little information is available about the development of root system of maize hybrids under different planting methods. It was hypothesized that ridge sown maize performs better and produces higher grain yield owing to the well-developed root system with higher root length and more root proliferation.

Ridges provide appropriate soil conditions like proper aeration and adequate availability of moisture essential for emergence that resulted in more plant population compared with flat seedbed [137, 138]. Likewise, ridges and beds provided loose fertile soil with more aeration and moisture availability and less mechanical compaction that permitted roots to grow profusely with more length, better proliferation and root growth rate. Chassot and Richner [139] reported that more bulk density or dense surface soil layer is a limiting factor for root growth resulting in less root length and concentrate the roots near the soil surface. Better root system enhanced the water and nutrient uptake resulting in a high leaf area index (LAI). LAI indicates the size of the assimilatory system of the crop, which captures solar radiation for carbon assimilation; higher LAI thus provides more area for photo assimilation resulting in higher crop growth rate. Liang *et al.* [84] reported that soil variation may explain environmental by cultivar interactions for several cultivars of winter wheat and winter barley. Lee and Spillane [140] also reported that both cultivar and fertilization management must be considered for optimum crop yield and quality in fields with different soils.

Several authors reported increase yields of some crops grown on vertisol due to the use of the broad-bed and furrow (BBF) as compared to the flatbed (FB) [141-143]. According to Gemechu *et al.* [144], the trials under FB conditions suffered a 20-50% yield reduction as compared to BBF. The same authors indicated that with the improvement of drainage conditions, the crop yield increases in 59.2% and 64.9% for local and improved cultivars. The camber beds (CB) and ridges and furrow (RF) drainage methods gave 151.7 and 80.6% seed yield increments over the FB, respectively, this indicates that the use of appropriate surface drainage methods contributes to seed yield increments of vicia species under waterlogged conditions [145]. Experimental findings also showed that planting chickpea, lentil and faba bean on BBF resulted in grain yield increments compared to un-drained FB conditions [146]. According to Getachew and Woldeyesus [147] findings, the highly significant drainage method by variety interaction for seed yield could be due to the greater yield of improved varieties under improved drainage conditions compared with FB conditions. Drainage by year interaction effects for seed yield of vicia species varied significantly ($P<0.05$) as indicated in Fig. 3.

The genotypes respond differently to the application of organic and inorganic fertilizers. Ahmad *et al.* [148] observed that plant height and leaf area of wheat significantly increased by combining organic and inorganic N fertilizers. Manure is a source of nutrients, which are released through mineralization, thus supplying the necessary elements for plant growth [149] and when combined with inorganic fertilizers it increased nutrient supply which enhanced vegetative growth, affecting plant height and yields [150]. Ahmad *et al.* [148] observed that root length and nutrient uptake of wheat increased significantly by combining organic manure and chemical fertilizer, which ultimately enhanced grain and straw yields. Similarly, an increase from 83.9 to 108.7% in yield of maize grain was recorded with the integration of organic and inorganic fertilizers [151]. Chiroma *et al.* [152]

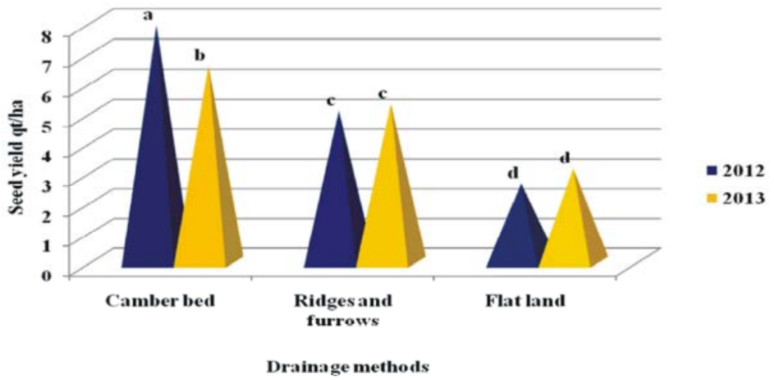

Fig. 3: Drainage by year interaction for seed yield of *Vicia* species. Source: [145]

reported that the improved growth and yield of maize in the farmyard manure (FYM) combined with N fertilizer were attributed to greater soil water content, higher nutrient availability and more protection from erosion compared to control treatment. The enhanced growth observed in the FYM treatments over the control could be partly due to a more favorable moisture regime in the root zone and partly due to the more efficient utilization of nutrients released from the decomposition of the added FYM [152].

Plant Factors Affecting GEI: The yielding ability of a genotype is the ultimate result of favorable interaction of genotype with the environment. Environmental factors such as soil characteristics and types, moisture, sowing time, fertility and temperature and day length vary over the years and locations. There is a strong influence of environmental factors during various stages of crop growth [153], thus genotypes differ widely in their response to environments. The adaptability of a genotype over diverse environments is usually tested by the degree of its interaction with different environments under which it is planted. A genotype or variety is considered to be more adaptive or stable if it has a high mean yield but a low degree of fluctuation in yielding ability when grown over diverse environments [154]. Specific response of a genotype may be observed in a particular environment and its stable performance over the different environments is a desirable characteristic. This depends upon the magnitude of GEI [155]; a genotype is considered to have agronomically stable if it yields well concerning the productive potential of the test environment [156]. Stability in the performance of a genotype over a range of environments is a desirable attribute and depends upon the magnitude of GEI [155]. Many research workers are of the view that average high yield should not be the only criteria for genotype superiority unless its superiority in performance is confirmed over different types of environmental conditions [157-160]. GEI for various traits have previously been studied by different researchers in various crops including chickpeas [161, 154], dry beans [162], hard winter wheat [163] and sunflowers [164].

Changes in the environment have been important determinants in genotypic performance, identifying the genotypes that can tolerate the changes in the environment are important [165]. The components of GEI have been recommended for commercial cultivation to get higher yields [166]. The quantitative properties, such as grain yield, in different plant genotypes grown in a wide environment, vary from one environment to another [167]. This phenomenon leads to get different production results from the GEI in different cultivation conditions [168]. The effects of GEI at significant levels reduce the relationship between genotypic values, preventing the genetic progression expected in breeding, which aim to breed high-quality genotypes [169]. Yadav *et al.* [170] determined that GEI was statistically significant concerning the studied parameters. High productivity and adaptability to the environment depend on the physiological responses of cultivars used in certain environmental conditions [171]. Atta and Shah [172] found significant differences in grain yields among genotypes, attributed to these differences to the magnitude of genotypes responses to the environments. According to Farshadfar *et al.* [6] found out that the environmental effect on yield was 86.44%, whereas the effects of genotype and GEI were only 2.48% and 11.08%, respectively.

The presence of the GEI indicates that the phenotypic expression of one genotype might be superior to another genotype in one environment but inferior in a different environment [173]. The GEI determines if a genotype is widely adapted for an entire range of environmental conditions or separate genotypes must be selected for different sub environments. When GEI occurs, factors present in the environment (temperature, rainfall, etc.), as well as the genetic constitution of an individual (genotype), influence the phenotypic expression of a trait. The impact of an environmental factor on different genotypes may vary implying that the productivity of plants may also vary from one environment to the next. Breeding plans may focus on the GEI to select the best genotype for a target population of environments. A basic principle indicated by the GEI is that even if all plants were created equal (same genotypes), they will not necessarily express their genetic potential in the same way when environmental conditions (drought, temperature, disease pressure, stress, etc.) vary. This important concept may require genetic engineering of plants specifically tailored to their environmental conditions.

The differences between the locations for performance of varieties for growth and yield traits are an indication of the reaction of genotypes to environmental changes. Arshad *et al.* [174] has already reported highly significant GEI in chickpea. The difference between genotypic means for all the traits at different locations indicated the significance of variation for production conditions. The effects of environments on the productivity of chickpea have been demonstrated by many researchers [174-176]. Significant genotypic, environment and GEI effects were recorded for most measured characters of Indian mustard suggesting the presence of substantial variability in the experimental materials, moreover, the environment significantly influenced all the characters and genotypes had a differential response to the environments [177]. Seed yield performance of common bean cultivars varying in growth habit and seed size at different parts of Ethiopia and reported as the occurrence of significant GEI and diversity of environments and cultivars [178-180]. The significant GEI results from changes in the magnitude of the differences among genotypes in different environments or from changes in the relative ranking of the genotypes. GEI accounted for 32% of the total sum of squares for grain yield, more than six times the magnitude of variation due to the main effect of genotype [29]. This dominant contribution of GEI relative to genotypic variation is consistent with other studies in rainfed lowland rice [181, 182]. Thus, the selection of better-adapted genotypes for the rainfed lowland ecosystem is complex because of large GEI, as discussed by Cooper [182].

Photosynthesis is closely related to dry matter production in most crops and plant responses and adaptation to abiotic stresses are reflected in changes in photosynthetic rates. Gimeenez and Fereres [183] also reported drought-induced genotypic changes in photosynthetic efficiency due to changes in leaf area and leaf area duration in sunflower. Differences between genotypes in transpiration, on the other hand, might have resulted mainly from differences in leaf area development and stomata regulation. Under well-watered conditions, genotypes transpired more water, maintained more open stomata and high water use before flowering [184]. This result is also in line with that of Altýnbas and Sepetoglu [167] in which they stated that the responses of the characters vary depending on the environment. The differences among the cultivars were of great importance because all investigated properties of the cultivars showed similar behaviors [185]. The degree of their reactions is not only dependent on their genotypic structure but also is affected by factors interacting with the genotype and environment [186, 187]. Therefore, different genotypes in different environments may show different performances [188]. It was reported that the yield and certain properties of plants showed significant variations depending upon the environment, most likely, affecting the yield at significant levels [189, 190]. The significance of GEI was also determined in the studies of Arshad *et al.* [174]; Abbas *et al.* [191]; Ali and Sarwar [192] and Karasu *et al.* [193], on chickpeas, white beans, green peas and soybeans, respectively.

CONCLUSION

When genotypes are introduced into new and diverse production environments, the occurrence of significant genotype by environment interaction (GEI) complicates the selection of stable genotypes. GEI is the differential phenotypic performance of genetically uniform genotypes across test environments. It occurs because different genotypes have varying genetic potentials to adjust themselves to variable environments. Knowledge of the nature, pattern and causes of GEI is vital in plant breeding, including varietal development, parent selection, establish breeding objectives, identify ideal test sites and formulate recommendations domains that can optimize adaptation. The analysis of variance doesn't give adequate and reliable information to make decisions in the varietal selection program if the GEI is statistically significant. The presence of significant interactions makes it difficult for breeders/agronomists to decide the variety for a recommendation. An inadequate number of locations and years can increase the chance of a wrong decision. If the number of genotypes, locations and years is increased, data handling would be a very difficult task, particularly in case of significant interactions. Generally, GEI is a common phenomenon in a variety of trials and its presence usually complicates variety selection and release decision.

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