



REVIEW ARTICLE

# Adapting cucurbits to diverse environments: Insights from GEI studies

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## Abstract

Recently, there has been increasing concern about crop failures and yield gaps attributed to climate change, as certain genotypes fail to achieve the desired yields or quality due to variations in external temperatures. To address this issue, breeders are working to develop climate-resilient varieties by incorporating relevant genes into cultivars or genotypes or by utilizing desirable source plants in the breeding process. Additionally, management practices are being implemented to mitigate environmental impacts. Multi-environmental trials (METs) are commonly employed by breeders to assess the adaptability of specific genotypes or cultivars across different locations and time periods. The data collected from these trials is then analyzed using stability statistical models designed for stability analysis, which allows for the evaluation of cultivar or genotype performance under varied environmental conditions. Over the past six decades, there has been a significant focus on modelling genotype-environment interactions (GEI), leading to the development of various mathematical methods and models to decipher GEI in METs, often referred to as "stability analysis." In the era of omics, phenomics techniques have emerged as valuable tools for screening morphological and physiological variations in genotypes resulting from environmental factors. This review emphasizes the importance of GEI in cucurbits, highlighting how environmental stress can alter physiological traits such as stomatal conductance, single leaf area, rooting depth and membrane composition. Furthermore, it notes the accumulation of stress-related proteins under stress conditions, underscoring the significance of understanding GEI for effective crop management and breeding programs.

## Keywords

cucurbits; environment; genotype; phenomics; stability; statistics

## Introduction

To mitigate the adverse impacts of climate change on agricultural stability, it is imperative to enhance the inherent traits of crops, enabling them to adapt to these environmental shifts (1). Crop infestations by pests and diseases often lead to reduced yields and diminished produce quality, while failures to meet yield projections disrupt the supply chain. Achieving sustainable food security requires both accelerating the rates of yield improvement (2) and reducing on-farm yield gaps (3). The ability of a crop to reach

its maximum genetic potential is contingent upon the environment in which it completes its life cycle.

The manifestation of a phenotype is closely linked to the interaction between the genotype, environment and the unique phenotypic responses of genotypes to varying environmental conditions, known as genotype-environment ( $G \times E$ ) interaction. The variation between the observed phenotype and the genotype-environment value is defined as the  $G \times E$  interaction (4). These interactions results in different responses among genotypes under diverse environmental conditions (5). Understanding and quantifying the factors driving such interactions is crucial for developing  $G \times E$  strategies that optimize production within specific environmental contexts (6, 7). Consequently, METs are essential for analyzing variations across different environments for a given cultivar.

Cucurbits, indigenous to India, are extensively cultivated throughout the nation, with cucumbers standing out prominently. The growth, development and productivity of these crops are shaped by both genetic makeup and environmental factors. Factors such as soil quality, climatic conditions, nutrient availability, cultural practices, diseases and pests exert profound influences on plant growth limitations (8, 9). The Cucurbitaceae family, encompassing major species like *Cucumis sativus* (cucumber), *Cucumis melo* (muskmelon), *Cucumis lanata* (watermelon) and various squashes, stands as the largest among highly diverse plant families (10, 11).

This review endeavours to assess genotype-environment interactions ( $G \times E$ ) within cucurbit genotypes, elucidating the dynamic interplay between genetic composition and environmental factor with a particular emphasis on discerning insights that enhance the adaptability and performance of cucurbit varieties across diverse environmental conditions.

### Environmental factors influencing yield and quality of cucurbits

To effectively utilize GEI in breeding programs, it is essential to understand the factors that cause varying responses

among cultivars due to GEI. These factors can be classified into 3 levels: optimal, suboptimal and super optimal. Differences in the rate of response increase among genotypes at suboptimal levels indicate efficiency variations, while differences in the rate of response decrease at super optimal levels reflect variations in tolerance (4).

Environmental factors influencing these responses can generally be divided into 2 categories: biotic (pests and diseases) and abiotic (temperature stress, ionic stress and water stress) (Fig. 1). Various strategies can help facilitate cultivar adaptation to these factors, including the development of resilient varieties, adoption of efficient management practices (such as direct water delivery to roots and optimized fertilizer application), grafting techniques to improve flood and disease tolerance and the use of soil amendments to enhance soil fertility and nutrient uptake.

A genotype that consistently delivers high-yielding performance across diverse environments likely possesses broad, durable resistance or tolerance to the biotic and abiotic factors encountered during its growth. A deeper understanding of crop environments enables breeders to select cultivars best suited to specific production conditions. High temperature stress during the flowering and fruit development stages of cucumber plants has been shown to reduce fruit set by 25–35%, fruit size by 15–25% and fruit quality (e.g., soluble solids content and firmness) by 10–20% across various cucumber genotypes (12).

### Multi-environmental trials-A glance

The breeding process can be viewed as comprehensive, multi-year efforts involving multiple cycles of data collection (13). METs are essential tools in this process, widely used to evaluate GEI across various crops. In METs, cultivars or genotypes are typically assessed using randomized complete block designs, with each environment having more than two replications (14). This precise approach allows for the identification of genotypes that exhibit minimal variability or maintain stability across different locations.

The primary objective of METs is to identify high

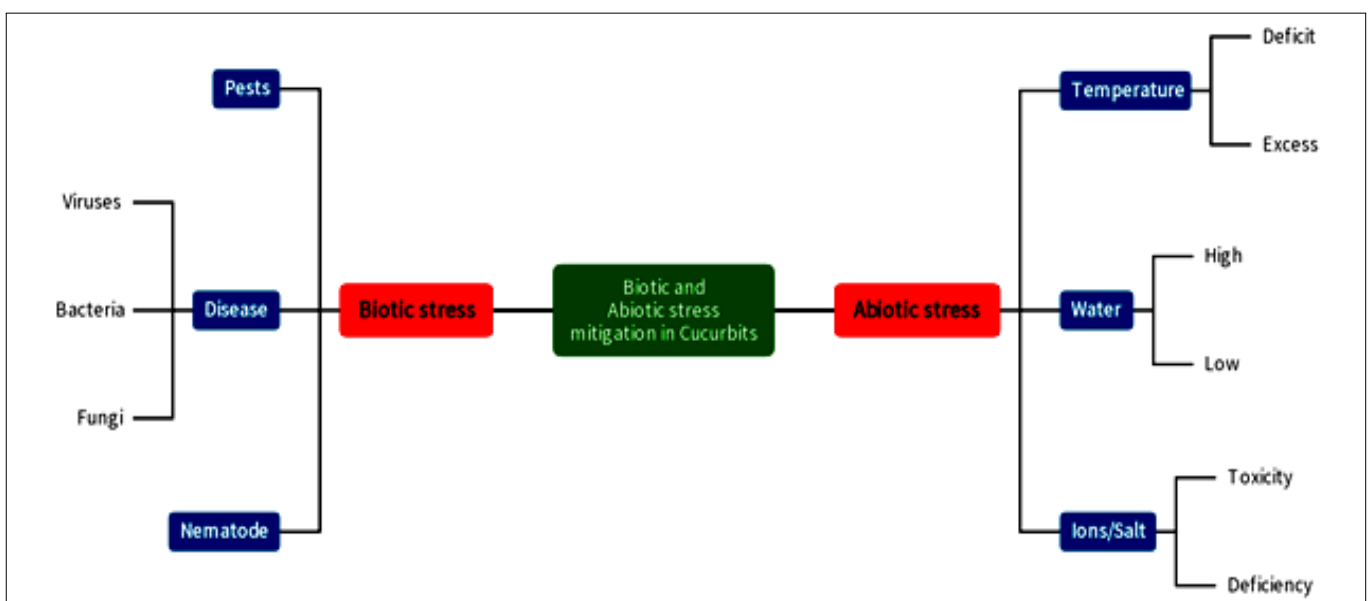


Fig. 1. Various forms of biotic and abiotic stress in cucurbits.

yielding, stable genotypes across diverse environmental conditions, separating the experimental data into environmental (E), genotype (G) and  $G \times E$  components. Despite the inherent variability of different environments, breeders prioritize evaluating genotypic effects and  $G \times E$  interactions to streamline the selection of cultivars in breeding programs. This focus allows breeders to establish homogeneous production units (HPUs) that closely mimic real world production environments, thereby guiding crop improvement efforts through the complexities of  $G \times E$ . A genotype that consistently performs at a high yield across varied environments is likely to possess broad, durable resistances or tolerances to both biotic and abiotic environmental factors encountered throughout its development.

In the context of cucurbit crops like pumpkin, squash and watermelon,  $G \times E$  studies have provided crucial insights to support breeding initiatives. By integrating multi-omics data with detailed phenotypic measurements, researchers have unraveled the complex interactions between genetics, biochemistry and the environment that influence key traits in pumpkin (15). Similarly, the intricate relationship between genotype and environment in cucumber has been explored using phenomics and omics approaches to examine  $G \times E$  dynamics (16). The power of integrating hyperspectral imaging and metabolomics to assess physiological responses in cucumber under varying environmental conditions was further demonstrated (17).

$G \times E$  studies in cucurbits have revealed responses to both biotic and abiotic stresses, in addition to yield and quality traits. Detailed research has explored the phenotypic and transcriptomic profiles of pumpkin under various disease pressures, including *Alternaria*, powdery mildew and yellow vine disease (18). Similarly, molecular and biochemical responses of watermelon to temperature stress and downy mildew disease have been investigated (19, 20). The integration of multi-omics data with comprehensive phenotyping enables a holistic dissection of  $G \times E$  interactions in cucurbit crops, paving the way for the development of resilient, high performing cultivars.

Additionally, studies on  $G \times E$  interactions in other cucurbit crops have provided valuable insights. For example, the stability and adaptability of bitter melon (*Momordica charantia*) genotypes across multiple environments were investigated, identifying genotypes with both broad and specific adaptability (21). The  $G \times E$  effects on yield and quality traits in bottle gourd (*Lagenaria siceraria*) were examined, offering guidance for targeted breeding efforts (22). Similarly,  $G \times E$  dynamics in ridge gourd (*Luffa acutangula*) were explored, underscoring the importance of identifying stable, high performing genotypes for diverse agro-climatic conditions (23). A systematic overview of  $G \times E$  interactions is illustrated in Fig. 2.

### **Integrating variability and heritability studies with GEI in cucurbits**

Cucurbits, including cucumbers, melons, squashes, and pumpkins, are among the crops that exhibit a high degree of genetic diversity. This diversity presents a valuable op-

portunity for breeding programs aimed at developing improved varieties. Understanding and utilizing this genetic diversity will depend on both genetic variability and heritability, particularly in how these characteristics interact with the environment, a phenomenon known as GEI.

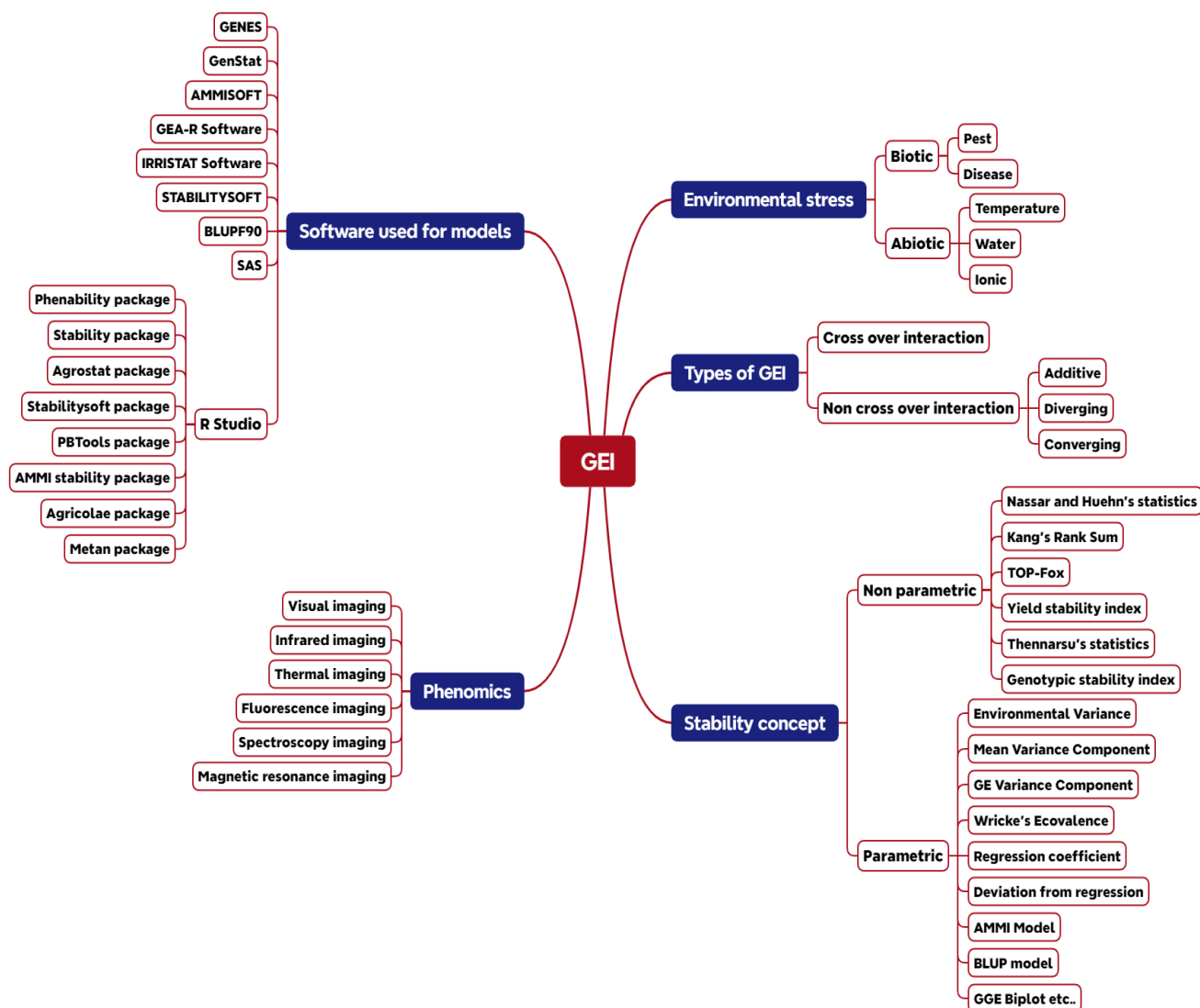
Genetic variability refers to the differences in genetic constitution among individuals within a particular species. This variation can be mapped using molecular markers such as simple sequence repeats (SSRs) and single nucleotide polymorphisms (SNPs). For instance, studies on the genetic characteristics of cucumbers have utilized these markers, which helped identify typical genetic traits that can be further applied in breeding programs (24). A systematic overview of  $G \times E$  interactions is illustrated in Fig. 2.

Heritability refers to the proportion of variation in a trait, such as fruit size or disease resistance, that is attributable to genetic factors. High heritability suggests that selecting for these traits in breeding programs will likely be successful. For example, in melons, traits like fruit firmness and sweetness have been found to have high heritability, indicating their suitability for effective selection in breeding efforts (25).

Studies on GEI evaluate the performance of different genotypes across varying environmental conditions. This is important because genotypes that perform well in one environment may not necessarily excel in others. By integrating GEI data with studies on genetic variability and heritability, breeders can either select traits that are stable across multiple environments or traits specifically suited to certain conditions. For example, QTL mapping in cucumbers identified genes responsible for resistance to *Pseudoperonospora cubensis* (26). Understanding how these resistance genes interact with the environment can aid in developing more resilient and disease resistant cucumber varieties.

Genetic variability, heritability and GEI collectively equip breeders with the insights needed to make informed decision when selecting parent plant and developing new variety. This comprehensive approach ensures that the resulting varieties not only perform well under given conditions but also remain resilient across a wide range of environments. By adopting this holistic strategy, breeders can develop robust, adaptable, high-yielding cucurbit varieties.

A study assessing the genetic variability in cucumber genotypes recorded significant values for the phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV) across major traits, indicating substantial genetic diversity. The highest PCV was observed for yield per plant (34.57%) and fruit flesh thickness (31.00%), while the GCV values were also notable, with yield per plant at 33.48% and fruit flesh thickness at 29.91%. High heritability estimates were found for all traits, particularly vine length (99.20%) and number of nodes per plant (97.90%), suggesting that these traits are predominantly controlled by additive gene action. Genetic advance as a percentage of the mean was substantial for



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**Fig. 2.** Systematic overview of the GEI in plants and the mitigation pipe line.

average fruit weight (132.22%) and vine length (74.96%), indicating significant potential for improvement through selection. This study underscores the importance of understanding genetic parameters such as GCV, PCV, heritability and genetic advance in developing effective breeding strategies for improving cucumber yield and quality traits (27).

### **Cucurbits genome, genetic variation**

Advancements in sequencing technologies and computational biology have significantly transformed whole genome sequencing strategies in plant sciences. Previously, due to the high cost of reagents and the limited capacity of Sanger sequencing, genomic applications were largely restricted to a few model organisms, such as *Arabidopsis thaliana* and *Oryza sativa* (28, 29). However, a major breakthrough came in 2009 when cucumber (*Cucumis sativus* L.) became the first member of the Cucurbitaceae family to have its genome sequenced. This achievement was made possible through a combination of Sanger sequencing and Illumina next-generation sequencing platforms, marking a significant milestone in plant genomics (30).

The latest advancements in sequencing technolo-

gies have significantly reduced costs and improved efficiency, leading to the successful sequencing of several economically important Cucurbitaceae crops, including *Cucumis melo* (melon), *Cucurbita pepo* (zucchini), *Cucurbita maxima* (pumpkin) and *Citrullus lanatus* (watermelon) (31). Additionally, recent developments in third-generation sequencing technologies by companies like Oxford Nanopore and Pacific Biosciences have facilitated the completion and continuity of genome assemblies (32).

The assembly of various Cucurbitaceae genomes has provided valuable insights into genetic diversity, evolutionary history and domestication processes (33, 34).

The evolution of plants in the Cucurbitaceae family has been significantly influenced by a series of whole genome duplication (WGD) events. The earliest of these, CucWGD1, occurred approximately 115–130 million years ago, laying the foundation for the development of this entire family (35). This was followed by CucWGD2, which affected crops within the Cucurbitaceae tribe, including important species like *C. pepo*, *Cucurbita moschata* and *C. maxima* (36, 37). Additionally, CucWGD3, which occurred in the Sicyoeae tribe and includes chayote (*Sechium*



edule), represents a more recent WGD event that took place around 25 million years ago (38).

Phylogenetic analysis suggest that *Siraitia grosvenorii* (luo-han-guo) was the first species to diverge from their common ancestor, closely followed by bitter melon (35). Despite utilizing Bayesian methods to estimate divergence times among these species, significant discrepancies remain. For instance, estimates for the divergence between cucumber and melon vary widely, ranging from 4 to 14 million years ago (38, 39). These inconsistencies highlight the complexities researchers encounter when attempting to accurately trace the evolutionary history of Cucurbitaceae plants.

Whole-genome sequencing of Cucurbitaceae has greatly enhanced our understanding of the genetic foundations underlying key fruit and vegetable quality traits (30, 40, 41). Researchers have identified and annotated thousands of coding genes linked to important characteristics such as pathogen resistance, fruit size, mass, colour, texture, length, shape, rind structure, ripening behaviour, sugar content, bitterness, flavour, aroma, sex determination and tendril development. Population analysis and genome-wide association studies (GWAS) on diverse species accessions have revealed numerous candidate genes responsible for these desirable traits in fruits and vegetables (40). This research is essential for guiding effective breeding strategies and contributes significantly to the development of high quality, resilient elite cultivars within the Cucurbitaceae family (30, 42).

#### **Approaches for investigating genotype by environment interactions-Stability concepts**

Stability is a pivotal concept in breeding analyses, encompassing two primary perspectives: static and dynamic (43, 44). The static concept suggests minimal variation in a cultivar's response across different environments, which is beneficial from the farmer's viewpoint and is considered the biological concept of stability (45). This is also referred to as type 1 stability (46). Conversely, the dynamic perspective indicates that a cultivar exhibits stable performance under varying environmental conditions, aligning with the agronomic concept and equivalent to type 2 stability (45, 46).

Numerous statistical models have been developed to analyze and interpret genotype-environment interactions, which can be broadly categorized into parametric and non-parametric stability statistics. Parametric stability statistics rely on distributional assumptions regarding environmental and genotypic effects and are further classified into univariate and multivariate approaches. Non-parametric or analytical approaches, on the other hand, estimate stability based on mean trait values and genotype rankings, without specific modeling assumptions. This approach minimizes bias from outliers, is user-friendly, and allows for straightforward interpretation. Furthermore, the addition or removal of genotypes has a minimal impact on the results (47). For breeders primarily concerned with rank order differences across environments, non-parametric statistics presents an excellent

alternative to parametric stability statistics (48).

#### **Parametric statistics**

Parametric statistics are essential tools for evaluating genotype stability, focusing on how different genotypes (like crop varieties) respond to various environmental factors, such as rainfall, temperature, osmotic stress and soil type. These statistics are most effective under specific conditions: the data should follow a normal distribution, and the errors and their interactions must exhibit consistent variance. However, if these assumptions are not met, parametric statistics may not provide the most reliable assessment of genotype stability (49).

The researchers identified that several parametric methods are employed to identify genotype stability (50). These include the regression coefficient ( $b_i$ ; 51), variance of deviations from the regression ( $Sd_i^2$ ; 52), Wricke's ecovalence stability index ( $Wi^2$ ; 53), Shukla's stability variance ( $\sigma_i^2$ ; 54), environmental coefficient of variance (CV $_i$ ; 55), Plaisted and Peterson's mean variance component ( $\theta_i$ ; 56), Plaisted's GE variance component ( $\theta(i)$ ; 57), and the yield-stability index (YS $_i$ ; 58). These methods enable the comparison and selection genotype stability across multi-environmental trials based on the collected data.

#### **AMMI-Based stability statistics**

The additive main effects and multiplicative interaction (AMMI) model provides a comprehensive analytical framework. This model integrates an additive model (ANOVA) for general means as well as means for genotypes (G) and environments (E), with a multiplicative model (PCA) for the residual of the additive model or GEI. The AMMI model has demonstrated effectiveness in various aspects, including understanding GEI, improving the accuracy of yield estimates, identifying mega-environment patterns, enhancing the flexibility of experimental designs and addressing missing data issues (59–61). The equation representing the AMMI model, which combines ANOVA and PCA analyses, is outlined as follows:

$$Y_{ij} = \mu + g_i + e_j + \sum_{n=1}^N \lambda_n \gamma_{in} \delta_{jn} + \rho_{ij} + \epsilon_{ij} \dots\dots\dots(\text{Eqn. 1})$$

Where,  $\mu$  represents the grand mean,  $g_i$  represents the main effect of genotypes  $i$ ,  $e_j$  represents the main effect of environment  $j$ ,  $\lambda_n$  represents the eigenvalue of the  $n^{\text{th}}$  interaction principal component analysis (IPCA) retained in the AMMI model,  $\gamma_{in}$  represents the eigenvector for the  $i^{\text{th}}$  genotype from the  $n^{\text{th}}$  IPCA,  $\delta_{jn}$  represents the eigenvector for the  $j^{\text{th}}$  environment from the  $n^{\text{th}}$  IPCA,  $N$  represents the number of IPC retained in the AMMI model,  $\rho_{ij}$  represents the GEI residual and  $\epsilon_{ij}$  represents the random error.

Various stability statistics derived from the output of the AMMI model have been proposed by the researchers. The yield performance of cucumber genotypes was investigated using the AMMI model, along with the geno-

type plus genotype-environment (GGE) approach (62).

### **BLUP-Based stability statistics**

Best linear unbiased prediction (BLUP) is widely recognized as the optimal methodology for estimating random effects within a linear model. By utilizing BLUP in conjunction with restricted maximum likelihood (REML), several parameters have been proposed to simultaneously measure performance and stability (63, 64). The first parameter, the harmonic mean of genotypic values (HMGV), identifies the genotype with the highest harmonic mean across environments, indicating stability. The second parameter, the relative performance of genotypic values (RPGV), serves as an adaptability index that measures the relative performance of genotypes across environments. The third BLUP-based parameter, the harmonic mean of RPGV (HMRPGV), combines stability, adaptability and mean performance into a single metric. In this context, unlike the AMMI model, the highest ranked values indicate stability.

The main objective of each study is to employ the appropriate method or model of analyses to effectively capture the GEI effect. While the AMMI and BLUP models are commonly utilized, each has its limitations. Superiority indices provide reliable estimates of genotype performance among various parametric AMMI- and BLUP-based stability parameters (65).

The GEI of 12 Piel de Sapo melon hybrids were investigated, focusing on their genotypic performance in terms of yield and °Brix content. Adaptability and stability were evaluated using the HMRPGV procedure (66).

### **GGE bi-plot**

The foundation for the GGE bi-plot methodology has been established, providing a theoretical framework that enables the visual analyses of genotype and phenotype evaluations (67, 68). Initially, genotypes are ranked based on their yield performance in specific environments. Conversely, when environments are static, genotypes are ranked according to their yield performance. This is followed by a comparison of the performance of genotype pairs. After identifying the best genotype in a particular microenvironment, its performance and effects in the macro-environment are studied, including stability analysis and comparisons of average performance. The discriminating ability and representativeness of test environments are assessed and visualization of these features for a subset of the data can be achieved by excluding certain genotypes or environments (69).

The GGE distance (GGED) and GGE instability index (GGEIN) can be calculated using the GGE bi-plot model. GGED measures the distance between the ideal genotype (stable/high performance) and each test genotype, while GGEIN approximates a genotype's contribution to the GEI. For example, nearly 36 genotypes were compared across three environments with varying drought conditions for fruit yield in melons (70).

### **Non-parametric statistics**

Non-parametric stability parameters offer several advantages, including ease of use and interpretation. They

are particularly beneficial because the addition or removal of one or a few genotypes does not significantly affect the results. For breeders primarily focused on differences in rank order across environments, these methods present the best alternative to the parametric models currently in use.

These non-parametric methods are especially useful as they provide ranks for various genotypes based on their yield. If a genotype maintains a consistent rank across diverse geographical areas, it indicates stability. The effectiveness of certain non-parametric methods in detecting genotype stability has been highlighted. Specifically, according to (71) Fox's top rank (FOX or Top-rank; 72), Nassar and Huehn's statistics ( $S_i^{(1)}$ ,  $S_i^{(2)}$ ; 73), which calculate the mean of the absolute rank differences of a genotype across all tested environments, as well as Kang's rank-sum (KR Kang; 74), Huhn's equation ( $S^{(3)}$  and  $S^{(6)}$ ; 49) and Thennarasu's statistics ( $NP^{(0)}$ ; 75) have been identified as valuable tools for assessing stability.

### **Software used to compute stability statistics**

Several software programs have been developed to facilitate the analysis of large datasets in breeding programs, particularly focusing on GEI. These tools utilize various scripting codes to expedite the interpretation of GEI effects and the selection of optimal genotypes within defined parameters. Among the widely used software are GENES, AMMISOFT, GEA-R, IRRISTAT, BLUPF90, STABILITYSOFT, SAS, GenStat, TNAUSTAT and R Studio. Notably, SASG  $\times$  E, RG  $\times$  E and R Studio's Metan package are dominant choices for conducting MET. These software applications play a crucial role in ensuring precise and accurate analysis of GEI data, thereby aiding breeders in making informed decisions for crop improvement programs.

### **Phenomics: High throughput phenotyping (G $\times$ E)**

In 1949, the term "Phenome" was introduced to encompass all of a cell's non-genetic, non-self-replicating components, representing the complete set of observable traits of an organism. In contrast, the genome is recognized as the genetic foundation of the genotype (76). Phenomics is defined as the process of collecting extensive, high-dimensional phenotypic data across an entire organism (77). In recent years, significant exploration has been conducted into the reasons for and methods of measuring genomics, with technological advancements now poised to help address questions related to the measurement of whole-plant phenotypes in the future (78). Over the past decade, plant phenomics has made remarkable progress due to advancements in imaging and sensor technologies that facilitate the measurement of diverse traits and phenotypic variations in response to environmental influences and genetic changes (79). In plant science, plant phenotyping refers to the range of techniques and procedures employed to accurately evaluate plant growth, architecture and composition at multiple scales (80).

Multiple genes and their respective products interact in complex ways with different environments at various developmental stages, influencing an organism's performance (81). Recent advances in sensor technologies

enable the capture of plants' environmental histories and dynamic behaviors. With the successful sequencing of the genomes of *Arabidopsis* and several other crops, the next task is to map all phenotypic variations in major crops and identify key functional genes or quantitative trait loci (QTLs) to enhance these crops' genetic bases. Genome-wide phenotyping platforms will be crucial in achieving this objective (31).

The phenotype reflects the highly adaptable variations that emerge from genetics (G), environmental factors (E) and the interaction between genetics and the environment (G × E) (82). "Omics" data can be analyzed separately or combined through multi-omics approaches to provide insights into key questions in plant research (83). Phenomic data play a crucial role in unraveling the pathways that connect genotypes to phenotypes, aiding in the identification of the root causes of complex traits in crop yields and diseases. A fundamental aspect of phenomics involves collecting relevant phenotypic data across various levels of biological organization to capture the full spectrum of potential phenotypes associated with a specific genome. Consequently, plant phenotyping can be categorized based on its resolution and scale, ranging from the molecular level to the entire plant, as well as across different environments, from controlled laboratory conditions to field settings (77, 84).

Evaluating traits associated with physiological responses to abiotic stress in field conditions remains a significant challenge, hindering the progress of large-scale crop improvement efforts (85). Given the changing climatic conditions, identifying the key factors of specific target genotypic populations in various environments and selecting advantageous traits from available genetic resources has become increasingly difficult for plant breeders. Genomic selection and physiological breeding now necessitate accurate, high-throughput phenotyping (HTP) to leverage indirect traits for yield enhancement. While in-field HTP is gaining traction, its expansion for multi-environment trials poses challenges. Combining data science, HTP and modeling can help address this issue. Plant breeders must refine their strategies to improve selection accuracy under abiotic stress, ensuring crop resilience amidst growing variability (86).

Government institutes in India, such as ICAR-IIHR, NIASM, CRIDA and IARI, provide phenotyping facilities that utilize the LemnaTec 3D Scanalyzer platform, which includes Scanalyzer 3D VIS, Scanalyzer 3D NIR and Scanalyzer 3D IRT sensors. Various ground and aerial phenotyping methodologies have been developed for crop phenomics studies, including the use of drones to phenotype plant populations. This type of phenotyping employs several imaging sensors, including visible imaging, infrared imaging, thermal imaging, fluorescence imaging, spectroscopy imaging and magnetic resonance imaging. These sensors can be used individually, allowing for separate plant and root phenotyping. In addition, specific instruments are employed for rhizotrons, minirhizotrons, rhizoponics and clear pot methods to facilitate 3D phenotyping (87).

Pumpkin traits, such as root diameter, length and density, were studied using RGB-D sensors in underground platforms, while cucumber traits, including plant height and leaf area, were also evaluated with the same technology (15, 16). Hyperspectral sensors were used to estimate nitrogen, magnesium and potassium levels in cucumbers (17). Research on pumpkins addressed biotic stress factors, including *Alternaria*, powdery mildew, anthracnose and yellow vine disease. In contrast, studies on watermelons focused on abiotic stress (temperature) and biotic stress (anthracnose, downy mildew), utilizing RGB sensors (18–20).

#### ***GEE studies in cucurbits***

The study aimed to evaluate fifteen parent lines, thirty six hybrids and three standard checks to estimate the nature and magnitude of genotype-environment interaction and the correlation among various stability parameters in *Cucumis* lines. This was conducted using a randomized block design with 3 replications at 3 locations: Udaipur, Banswara and Chittorgarh in Rajasthan. The results indicated that the hybrid L3 × T3 had the highest fruit weight, measuring 1385.67 g and a fruit diameter of 11.82 cm across the environments. Additionally, the hybrid L6 × T2 exhibited the maximum fruit length of 34.30 cm in the same environments (88).

In a study using the AMMI model and GGE bi-plot to assess cucumbers, which are valued for their health benefits and have been shown to yield better during the dry season due to their high water content, 5 genotypes were tested: Ashley (ASL), Market More (MM), Marketer (MK), Poinsett (P.ST) and Super Marketer (SM). These genotypes were evaluated across 4 environments: Calabar, Ikom, Obudu and Obubra in 2015. The lowest yields were recorded for Market More at 13.96 t ha<sup>-1</sup> and Super Marketer at 16.66 t ha<sup>-1</sup>. The environment accounted for 59.60% of the total variation, with Ikom and Obudu identified as the most favourable environments for cultivation (89).

The yield and stability of 22 cucumber genotypes were evaluated over 3 consecutive years across 24 environments. The hybrid varieties 'Marbel F1' and 'Gy 14' exhibited the highest marketable yields, producing 23.6 t ha<sup>-1</sup> and 22.5 t ha<sup>-1</sup>, respectively. 'Marbel F1' also demonstrated an early yield of 10.5 t ha<sup>-1</sup> with an average of 1.8 fruits per plant, while 'Gy 14' had an early yield of 9.8 t ha<sup>-1</sup>, yielding 1.7 fruits per plant. The hybrids displayed good stability in traits, in contrast to inbred varieties, which showed greater variability. These results support the potential for breeding stable, high yielding cucumber genotypes, benefiting breeders and seed producing companies, and contributing to enhance agricultural productivity and food security (90).

GGE bi-plot analysis of 18 "egusi" melon accessions identified DL99/75 as one of the standout accessions regarding yield performance across multiple environments. Additionally, DD98/506 and DL99/76 also demonstrated high performance, especially in the Abeokuta 2 environment. The results demonstrated the significance of genotype-environment interaction on yield, emphasizing the



need for strategic selection in breeding programs. This study provides valuable melon improvement in the context of changing climatic conditions and future research should focus on the stability and adaptability of these high performance accessions (91).

Nine genotypes of orange-fleshed melon were evaluated for their yield and quality attributes in south-central Texas over a 3 year period. The 'Journey' genotype emerged as the highest yielding genotype, achieving a total fruit yield (TFY) of 69.4 t ha<sup>-1</sup> and a marketable fruit yield (MFY) of 49.8 t ha<sup>-1</sup>. Among the TAMU breeding lines, 'TAMU 146' was notable for its consistent TFY. While 'TAMU OC' exhibited some yield variation, it excelled in soluble solids content (SSC) and fruit firmness, particularly at Weslaco. The 'Mission' genotype showed consistent performance across several traits, with an average beta-carotene content of 23.9 mg/g and a vitamin C level of 285.8 mg/g. These results underscore the significant genotype-by-environment interactions that can occur, highlighting the importance of this information for breeding programs aimed at improving the yield and quality of melons (92).

Twelve Piel de Sapo melon hybrids were evaluated in the Mossoró-Assú agricultural region of Brazil, using mixed to analyze genotype-environment interactions. The results were complex, revealing the challenges inherent in selecting superior genotypes. Using the HMRPGV approach, 2 excellent hybrid variants, HP-09 and HP-06, were identified for their high stability and yield—39.99 mg/ha and 34.72 mg/ha, respectively—with soluble solids content of 13.79 °Brix and 12.62 °Brix. These hybrids outperformed the commercial variety 'Sancho' and met the quality standards required by European markets, indicating their potential for production in the semiarid northeast region of Brazil (66).

Genotypes from the national plant gene bank of Iran were tested under water depletion levels of 25%, 50% and 75% of the soil moisture. AMMI and GGE analysis identified genotypes 11, 23, 28 and 33 as stable. Among them, genotypes 11 and 28 were the most stable, with genotype 28 showing outstanding performance under severe drought conditions, making it ideal for hybridization. This approach clarified the interactions involved in these genotypes, leading to the identification of stable varieties suitable for arid regions (70).

Fifteen cucumber genotypes were evaluated in a study conducted in Coimbatore. The experiment was designed as randomized block design with 2 replications across 5 different seasons, considering various growth and yield parameters. The results indicated that the genotypes CBECS-37 and CBECS-25 achieved the highest fruit yields of 620.07 g per plant and 589.25 g per plant, respectively. The genotype CBECS-5 had the highest TSS content at 5.15 °Brix, making it suitable for slicing purposes, while CBECS-12 also had a high TSS of 5.10 °Brix. This study underscores the significance of genetic diversity in cucumber breeding and opens avenues for future breeding programs focused on yield and quality improvement. The findings suggest

that selective breeding of cucumber variants can lead to varieties better suited for salad and slicing purposes, benefiting farmers and consumers (93).

All these genotypes were tested in a randomized complete block design across five environments, using Eberhart and Russell's and Perkins and Jinks' stability models to evaluate genotype performances. The highest and most stable genotype, PMM-97-19, had a fruit weight of 886 g, high yield and a TSS content of 12.8%. PMM-251 was also stable at a fruit weight of 850 g with a very high yield and TSS of 12.5%. Other stable genotypes included Pusa Madhuras (772 g), PMM-249 (859 g), PMM-208 (923 g) and PMM-266 (885 g). PMM-242 and PMM-191 were stable in terms of days to the first female flower. These findings emphasize the importance of selecting stable genotypes for reliable agricultural yield across various environments, ensuring high yields and acceptable TSS levels (94).

### Challenges and future research directions

Studying the interaction between plant genetics and the environment is particularly complex, especially with cucurbits like cucumbers, squash and melons. Traditional methods often fall short in capturing the wide range of variables influencing these interactions, leaving many aspects of the genetic and biological mechanisms in cucurbits unexplored (95). However, recent advancements in envirotyping and high throughput phenotyping technologies are providing deeper insights into how genes interact with their environment (96). These next-generation tools, which integrate genotype, environment and management ( $G \times E \times M$ ) factors, facilitate a more comprehensive understanding of this interaction (97). Incorporating advanced technologies such as artificial intelligence and machine learning can enhance predictive phenomics, improving breeding outcomes and addressing the challenges posed by environmental variations (98). This integrated approach, which combines optimized experimental designs with high quality field trials, will be vital in developing more resilient and productive varieties of cucumber, squash and melon, ultimately ensuring food security in the face of climate change.

### Conclusion

The Cucurbitaceae family encompasses a diverse range of nutritionally important crops cultivated worldwide. GEI plays a critical role in selecting genotypes for specific environments, making it essential for breeders to thoroughly study these effects to develop climate-resilient cultivars suited to particular adaptive conditions. To analyze genotype stability across different geographical areas, numerous statistical models and software tools are available. Phenomic techniques provide an accurate approach to cultivar development and evaluation and several Indian government institutes have established platforms for assessing crop responses to diverse environmental conditions. Moving forward, extensive research is needed to address environmental challenges affecting genotypes. The continued advancement of fast and precise plant phenotyping holds significant promise for improving vegeta-



ble cultivation, with potential benefits for both the environment and the economy. Ultimately, the integration of cutting-edge technologies and diverse research initiatives marks a transformative era in plant phenotyping, driving the adoption of sustainable agricultural practices.

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## Authors' Contributions

Writing original draft and resources collection were done by MB. Conceptualization, writing – review & editing, supervision, validation and resources were contributed by UNDH. The visualization process was carried out by PN, SA and GP. All authors read and approved the final manuscript.

## Compliance with Ethical Standards

**Conflict of interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

**Ethical issues:** None

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