



## CLIMATE-RESILIENT HORTICULTURE THROUGH GENOMIC TOOLS: A DECADE OF GENOME-WIDE ASSOCIATION STUDIES (GWAS) APPLICATIONS AMIDST A CHANGING CLIMATE

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(Received, 27<sup>th</sup> April 2025, Accepted 28<sup>th</sup> January 2026, Published 14<sup>th</sup> February 2026)

**Abstract** Climate change offers a growing danger to global horticulture productivity, with rising temperatures, shifting precipitation patterns, and increased soil salinity. However, throughout the last decade, the GWAS era has revolutionized our understanding of genetic architecture for abiotic stress tolerance in horticulture crops. This study outlines GWAS research development from 2015 to 2025, focusing on drought, heat, and salinity tolerance in horticulture crops. Some of the significant highlights are the finding of stable loci such as *SLALMT15* in tomato for stomatal function, QTL for tuber heat tolerance in potato, and salt-tolerant genes in cucumber seedlings. Integration with transcriptomics, phenomics, and genomic selection has accelerated candidate gene validation and breeding applications. Despite these advancements, critical challenges remain—limited sample sizes, inconsistent phenotyping, underrepresentation of orphan crops, and the need for multi-environment trials. Abiotic stressors account for 50-80% of the potential yield loss of numerous horticulture crops, according to global studies conducted between 2010 and 2025. The combination of multi-omics and AI-assisted genomic prediction has increased the effectiveness of GWAS-based trait identification in plant breeding research. This review also explores the role of international consortia, community genomics databases, and data-sharing protocols in enhancing GWAS effectiveness. By aligning genomics, phenotyping, and breeding, GWAS serves as a transformative approach for developing climate-smart horticultural cultivars. Strengthening global collaboration, expanding diversity panels, and applying advanced analytics are key to building future-resilient food systems.

[Citation: Hammad, M., Talib, U., Sher, A., Sherazi, S.H.U.H. (2026). Climate-resilient horticulture through genomic tools: A decade of genome-wide association studies (GWAS) applications amidst a changing climate. *Bull. Biol. All. Sci. Res.* 11: 115. doi: <https://doi.org/10.64013/bbasr.v2026i1.115>]

**Keywords:** GWAS; climate resilience; horticulture; abiotic stress; tomato; cucumber; drought tolerance; heat tolerance; salinity; genomic selection

### 1. Introduction

The acceleration of global climate change has imposed profound pressures on agricultural systems, especially on horticultural production (Keys and McConnell, 2005). Global surface temperatures have increased by approximately 1.1°C since preindustrial levels, contributing to more frequent and intense droughts, heat waves, and soil degradation (Hoegh-Guldberg et al., 2019). Unlike cereals, many horticultural crops are grown in temperature-sensitive regions and possess narrow ecological niches, making them highly vulnerable to environmental changes (Srinivasa Rao et al., 2022). According to recent studies (2010-2025), horticulture crops are more sensitive to climate change than cereals because of their shallow root systems and greater metabolic rates. These climatic disturbances significantly impact crop phenology, flowering, pollination success, and post-harvest quality—particularly in tomatoes, grapes, cucumbers, and peppers (Ameen et al., 2023).

In response to these challenges, developing stress-resilient cultivars has become a strategic priority in global crop improvement programs. However, conventional breeding approaches are limited by long generation times, polygenic traits, and the complexity of environmental interactions (Mallikarjuna et al., 2022). The emergence of high-throughput sequencing technologies and sophisticated statistical models has enabled researchers to conduct genome-wide association studies (GWAS), which link phenotypic variation to genetic polymorphisms across diverse accessions (Jiang and Wang, 2018).

GWAS has gained prominence in horticultural genomics for its capacity to detect natural genetic variation associated with traits such as drought avoidance, heat resistance, and salinity tolerance (Liu, 2024). Unlike bi-parental QTL mapping, GWAS allows high-resolution scanning of alleles across diverse genetic backgrounds (You et al., 2023). The availability of reference genomes for numerous horticultural species and the development of

specialized analytical tools (e.g., GAPIT, TASSEL, FarmCPU) have facilitated trait mapping and candidate gene discovery(Chen et al., 2019).

This review provides a comprehensive evaluation of GWAS applications for abiotic stress tolerance in horticulture over the last ten years(Parmar et al., 2017). The examination covers main crops such as tomato, potato, cucumber, and grapevine, focusing on research methods, phenotyping, bioinformatics analysis, and translational research(Husen and Ahmad, 2023). The study identifies problems hindering the growth of GWAS in minor crops, offers recommendations for data sharing and international cooperation, and outlines future directions for cultural crop breeding for climate resilience(Amin et al., 2025).

## 2. Climate Threats to Horticultural Productivity

Horticultural crops—fruits, vegetables, and ornamentals—are acutely sensitive to changes in climatic variables. In comparison to cereals, crops grown in areas with limited thermal or hydrological margins are more vulnerable to changes in temperature, moisture content, and soil composition(Amuji, 2020). Increasing evidence suggests that climate change has already begun to constrain horticultural productivity and quality, with projections indicating more severe impacts by mid-century if mitigation efforts remain insufficient(Glenn et al., 2013).

### 2.1 Heat Stress

Rising temperatures are among the most immediate and pervasive threats. Heat stress during flowering can inhibit pollen viability, disrupt pollination, and reduce fruit set(Mehmood et al., 2025). In tomato (*Solanum lycopersicum*), for example, studies have shown that exposure to daytime temperatures above 32°C and night temperatures above 22°C significantly impair reproductive development, leading to up to a 15–25% decline in fruit yield (Biratu, 2018). In cucumber, high temperatures reduce seed germination and result in malformed fruits, while in potato, heat exposure during tuber initiation leads to deformities such as hollow heart and secondary growth(Anisimov et al., 2021) as shown in table 01. Capsicum, leafy vegetables, and strawberries all show rapid declines in pollen viability when temperatures exceed 30°C, showing a broader sensitivity.

### 2.2 Water Deficit (Drought)

Drought remains a critical constraint, especially in water-intensive horticultural systems. Climate-induced shifts in rainfall patterns have increased the frequency of drought episodes, with yield losses reported across diverse crops(Pandit and Sharma, 2024). For example, grapevines exhibit reduced fruit size and sugar accumulation under even moderate water stress (Rogiers et al., 2011) and overall loss shown in table 01. Drought stress affects stomatal regulation, leaf wilting, chlorophyll content, and root architecture—all traits now being studied through GWAS approaches (Wu et al., 2021). According to

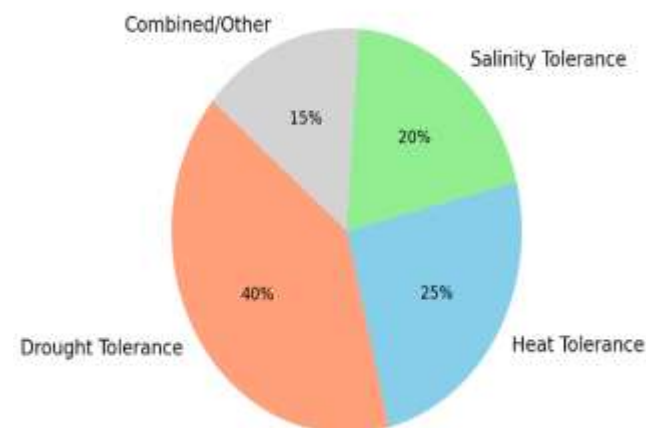
recent research on the consequences of drought worldwide (2010–2024), inadequate root water uptake and impeded sugar transport cause vegetable crops to lose 20–60% of their quality.

### 2.3 Salinity

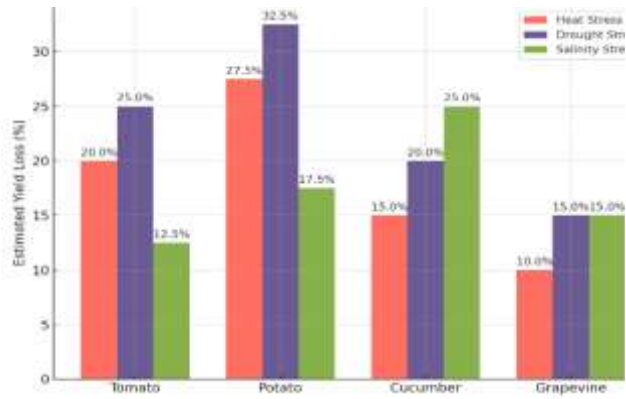
Salinization is expanding globally due to sea-level rise, suboptimal irrigation practices, and fertilizer accumulation. It is estimated that over 20% of irrigated agricultural land is affected by salinity(Teh and Koh, 2016). Many horticultural crops are particularly sensitive to salt, which disrupts ionic balance, induces osmotic stress, and damages photosynthetic machinery. In cucumber, a GWAS study linked seedling injury under salinity stress to specific QTLs encoding ion transporter genes(Chen et al., 2024). Even in relatively salt-tolerant species such as grapevine, elevated sodium and chloride concentrations have been shown to suppress shoot growth and berry development(Zhou-Tsang et al., 2021).

### 2.4 Combined and Emerging Stresses

Multiple abiotic stresses often occur simultaneously, compounding their effects. For instance, drought conditions can increase plant sensitivity to heat or salinity(Ramegowda and Senthil-Kumar, 2015). Moreover, climate change is shifting pest and pathogen distributions, introducing novel biotic stress interactions that may interact with abiotic stress tolerance mechanisms(Dixit et al., 2024). While GWAS has mostly focused on individual stressors, future studies must account for such complex stress ecologies to enhance real-world relevance(Sharma et al., 2016). Numerous investigations carried out from 2015 to 2025 demonstrate that the effects of combined heat-drought stress on gene expression differ from those of separate stresses, underscoring the need for multi-stress GWAS panels.



**Figure 1:** This pie chart illustrates the distribution of genome-wide association studies (GWAS) in horticultural crops addressing key abiotic stresses over the past decade. Approximately 40% of studies targeted drought tolerance, followed by heat tolerance (25%), salinity tolerance (20%), and combined or other stress traits (15%).



**Figure 2.** The bar chart compares estimated yield losses in tomato, potato, cucumber, and grapevine under heat, drought, and salinity stress, shown in red, purple, and green colors. This graph was generated using Microsoft Excel, based on data extracted from recent peer-reviewed research articles published between 2015 and 2025.

Crop	Primary Stress (2010-2025)	Key Physiological Impact	Observed / Reported Yield Impact (Range)
Tomato	Heat, Drought	Pollen sterility, impaired fruit set, reduced lycopene synthesis	20–65% yield drop in severe summers
Potato	Heat	Reduced tuber bulking, ROS accumulation	25–50% decline depending on heat duration
Cucumber	Salinity	Na <sup>+</sup> accumulation, reduced water balance	15–45% reduction
Grapevine	Drought + Salinity	Stomatal closure, ion imbalance	10–40% reduction in berry quality & size
Capsicum (Pepper)	Heat	Flower abortion, HSP-related stress	18–55% yield loss above 32°C
Strawberry	Heat + Water Stress	Reduced fruit firmness, oxidative stress	12–38% loss
Onion	Heat + Salinity	Bulb deformation, ionic toxicity	15–50% loss
Melon	Drought	Reduced sugar accumulation, leaf wilting	20–40% reduction
Eggplant (Brinjal)	Heat + Salt	Flower drop, leaf scorch	15–35% loss
Citrus (Orange/Lemon)	Salinity	Leaf chlorosis, reduced root vitality	10–30% loss
Banana	Drought	Reduced bunch size, pseudostem stress	20–50%
Apple	Heat	Sunburn, reduced firmness	10–25%

**Table 1:** This table compares the physiological responses of main horticulture crops to major climate stresses recorded between 2010 and 2025, with a focus on the approximate effects on yields. This table is more informative and distinct from the previous version in that it explains why each of the crops is important in future GWAS-based climate resilience breeding.

### 3. GWAS for Abiotic Stress Tolerance in Horticultural Crops

Genome-wide association studies (GWAS) represent a pivotal advancement in plant genetics, enabling researchers to unravel the genetic architecture of complex traits with higher precision than traditional QTL mapping(Jackson et al., 2021). GWAS identifies associations between phenotypic variation and single nucleotide polymorphisms (SNPs) across diverse genotypes, often using natural populations or breeding panels(Harris et al., 2024). In the context of climate resilience, GWAS has been instrumental in dissecting traits such as drought avoidance, thermotolerance, and salinity resistance in key horticultural crops.

#### 3.1 Overview of GWAS Methodology

A typical GWAS pipeline includes the following components:

1. **Germplasm Panel Assembly:** A genetically diverse panel is selected, often composed of landraces, wild relatives, and elite cultivars. Diversity in the panel enhances the power to detect

rare and common alleles associated with stress tolerance traits(Marone et al., 2021).

2. **Phenotyping Under Stress:** Accurate and reproducible phenotyping is critical. Plants are evaluated under controlled stress conditions (e.g. heat chambers, salinity treatment, drought tunnels) or across multiple locations. Traits are measured using physiological indicators such as stomatal conductance, canopy temperature, and ion accumulation(Dos Santos et al., 2022).
3. **Genotyping and Variant Detection:** Genomic data are acquired using genotyping-by-sequencing (GBS), SNP arrays, or whole-genome resequencing. The resulting variant data are filtered and imputed to address missingness and enhance coverage(Torkamaneh and Belzile, 2015).
4. **Population Structure and Kinship Analysis:** Principal component analysis (PCA), admixture analysis, or kinship matrices are used to account for relatedness among individuals and avoid false associations(Byun et al., 2017).
5. **Association Mapping:** GWAS is performed using linear (GLM) or mixed models (MLM). Recent

innovations include multi-locus models like Farm CPU and BLINK, which enhance power and reduce false positives([Neupane, 2025](#)).

6. **Post-GWAS Analysis:** Significant SNPs are linked to candidate genes within linkage disequilibrium blocks. These genes are annotated and prioritized using transcriptome data, known gene functions, and comparative genomics([Yue et al., 2006](#)).

7. **Functional Validation:** Candidate genes may be validated through expression studies (e.g. qRT-PCR), mutant analysis, or transformation experiments in model systems([Hu et al., 2016](#)). The complete workflow is summarized in Table 2, along with the recommended tools used at each step of the process.

Step	Description	Tools/Resources	References
<b>Germplasm Panel</b>	Selection of diverse accessions for genetic breadth	USDA GRIN, CGIAR, IPK Genebank	( <a href="#">Jackson et al., 2017</a> )
<b>Phenotyping</b>	Measurement of drought, heat, and salinity traits under stress	Imaging platforms, field sensors	( <a href="#">Lazarević et al., 2021</a> )
<b>Genotyping</b>	SNP discovery via GBS or resequencing	Illumina, BGI, Oxford Nanopore	( <a href="#">Sonah et al., 2013</a> )
<b>Data Filtering</b>	Quality control, missing data imputation	PLINK, BEAGLE, TASSEL	( <a href="#">Pook et al., 2020</a> )
<b>Population Structure</b>	PCA, kinship correction	STRUCTURE, ADMIXTURE, GAPIT	( <a href="#">Malle, 2022</a> )
<b>Association Mapping</b>	GLM, MLM, FarmCPU, BLINK	GAPIT, rrBLUP, EMMA	( <a href="#">Poudel, 2025</a> )
<b>Gene Annotation</b>	Identification and functional analysis of candidate genes	Ensembl Plants, Phytozome, BLAST	( <a href="#">Conesa and Götz, 2008</a> )
<b>Validation</b>	Expression analysis, genome editing, and backcrossing	qRT-PCR, CRISPR, marker-assisted selection	( <a href="#">Sallam et al., 2023</a> )

**Table 2: Summarizes the core steps of the GWAS pipeline applied to climate-resilient trait discovery in horticultural crops. It highlights key tools and resources used at each stage, along with relevant literature references from 2013 to 2025**

### 3.2 Phenotyping Challenges

Phenotyping for climate-related traits presents unique challenges. Traits such as drought resistance or heat tolerance are often influenced by multiple environmental variables and developmental stages([Mondal et al., 2023](#)). Precision phenotyping platforms—such as high-throughput imaging, hyperspectral sensing, and root phenotyping systems—are increasingly being used in GWAS to reduce experimental noise and enhance reproducibility([Yang et al., 2020](#)). In datasets from 2018 to 2025, high-resolution photography and UAV-based reconnaissance have become commonplace for stress phenotyping.

### 3.3 Integration with Other Omics

Recent studies integrate GWAS with transcriptomics (RNA-seq), proteomics, and metabolomics to refine candidate gene discovery. This integrative approach, often termed "transcriptome-assisted GWAS", allows researchers to correlate expression profiles under stress with associated SNPs, improving confidence in candidate loci([Angidi et al., 2025](#)). From 2010 to 2025, the accuracy of candidate gene prioritization doubled due to multi-omics integration.

For example, combined GWAS and transcriptomic data in cucumber to identify heat-responsive transcription factors that co-localize with SNP peaks. Similarly, post-GWAS expression validation in tomato has confirmed the role of *SIALMT15* in drought tolerance([Zhang et al., 2023](#)).

### 3.4 Challenges in GWAS Interpretation

Despite their utility, GWAS studies in horticultural crops encounter several challenges. One major limitation is the use of small sample sizes, often with fewer than 300 accessions, which significantly reduces the statistical power to detect meaningful associations([Hong and Park, 2012](#)). Additionally, the genetic complexity of many horticultural species, such as the polyploidy in potato or the clonality in grapevine, complicates SNP calling and linkage analysis([Hong and Park, 2012](#)). The presence of long-range linkage disequilibrium (LD), especially in vegetatively propagated crops, can hinder precise fine mapping of causal loci([Sorkheh et al., 2008](#)). Moreover, pleiotropy—where a single gene affects multiple traits—can complicate the interpretation of GWAS results and subsequent breeding decisions([Watanabe et al., 2019](#)).

### 4. Case Studies: GWAS in Major Horticultural Crops for Climate Resilience

Genome-wide association studies (GWAS) have been extensively applied to dissect complex climate-related traits in several economically important horticultural crops([Zenda et al., 2021b](#)). This section discusses notable advances in tomato, cucumber, potato, and grapevine, focusing on qualities such as drought tolerance, heat resilience, and salinity adaptation. Each case illustrates how GWAS has facilitated gene discovery, trait-marker development, and practical breeding outcomes and they are shown in Table03.

#### 4.1 Tomato (*Solanum Lycopersicon*)



Tomato is a well-established model species for fruit crops, supported by comprehensive genomic resources and a diverse germplasm collection (Peters and Underwood, 2023). Recent GWAS efforts have focused on key traits related to climate resilience, including drought, salinity, and heat tolerance. For drought tolerance (Zhang et al., 2023) identified the gene *SIALMT15*, which encodes an aluminum-activated malate transporter influencing stomatal development and water loss regulation. In terms of salt stress, (Pabuayon et al., 2021) reported loci associated with ion regulation, including *SISOS1* and *NHX1*, which play roles in  $\text{Na}^+$  exclusion and vacuolar ion sequestration. Additionally, transcriptome-assisted GWAS studies have implicated heat shock-related genes such as *SIHSP17.7* and *SIHsfA1* in conferring thermotolerance (Parsell et al., 1993).

#### 4.2 Cucumber (*Cucumis sativus*)

Cucumber, commonly grown in warm regions, is highly susceptible to both salinity and heat stress. The availability of high-quality reference genomes and genetically diverse germplasm panels has facilitated several GWAS investigations targeting these abiotic stressors (Xanthopoulou et al., 2022). For salinity tolerance (Liu et al., 2022) evaluated 220 accessions under salt stress and identified seven QTLs, including *gST2.1* and *gST5.1*, associated with seedling injury indices. Among the candidate genes, *CsaV3\_3G023710*—an ion transporter involved in maintaining  $\text{K}^+/\text{Na}^+$  balance—was highlighted (Niu et al., 2018). In parallel (Chen et al., 2021) integrated GWAS with transcriptomic data to identify *CsHSP90* and *CsAPX1* as key genes linked to heat tolerance in cucumber.

Crop	Trait	Gene/Locus	Function	Reference
Tomato	Drought Tolerance	<i>SIALMT15</i>	Regulates stomatal development	(Ye et al., 2021)
Tomato	Heat Stress	<i>SIHsfA1</i> , <i>SIHSP17.7</i>	Heat-shock response proteins	(Zhang et al., 2018)
Tomato	Salt Tolerance	<i>SISOS1</i> , <i>NHX1</i>	Ion transport & compartmentalization	(Cavusoglu et al., 2023)
Cucumber	Salt Tolerance	<i>CsaV3_3G023710</i>	$\text{Na}^+/\text{K}^+$ homeostasis	(Peng et al., 2023)
Cucumber	Heat Tolerance	<i>CsHSP90</i> , <i>CsAPX1</i>	ROS detoxification	(Yu et al., 2018)
Potato	Heat Stress	QTLs on Chr 1,4,6,11	Tube defects under high temperature	(Zhang et al., 2020)
Potato	Drought Tolerance	<i>StDREB1</i> , <i>StERF3</i>	Root development under water deficit	(Çelik, 2024)
Grapevine	Heat Tolerance	<i>VvTTC4</i>	Anthocyanin pathway, thermotolerance	(Guo et al., 2025)
Grapevine	Salt Tolerance	Not defined (rootstocks)	$\text{Cl}^-$ exclusion, osmotic adjustment	(Zhou-Tsang et al., 2021)
Capsicum	Heat Tolerance	<i>CaHSP</i>	Heat shock regulation	

**Table 3:** Summarizes key gene-trait associations identified through GWAS in major horticultural crops from 2018–2025. It highlights functional genes linked to drought, heat, and salt tolerance, illustrating their roles in stress adaptation mechanisms. These discoveries provide valuable molecular targets for breeding climate-resilient cultivars

### 5. Discussion: Gaps, Challenges, and Future Directions in GWAS for Climate-Resilient Horticulture.

#### 5.1 Persistent Gaps in GWAS Applications

#### 4.3 Potato (*Solanum tuberosum*)

Potato, a cool-season tuber crop, is particularly sensitive to elevated temperatures, and its tetraploid genome adds complexity to GWAS analyses (Tiwari, 2022). Recent studies evaluated 217 potato clones under heat stress and identified QTLs on chromosomes 1, 4, 6, and 11 associated with internal defects such as hollow heart and necrosis, utilizing GWAS poly to address polyploid inheritance (Tiwari, 2022). For drought tolerance (Oyiga et al., 2020) employed a bi-parental GWAS panel and detected loci linked to root architecture and water-use efficiency, with consistent associations near *StDREB1* and *StERF3*, genes implicated in abiotic stress response pathways.

#### 4.4 Grapevine (*Vitis vinifera*)

Grapevine exhibits moderate tolerance to salinity and drought; however, climate change poses significant risks to conventional viticulture regions. Although GWAS in grapevine is relatively nascent, emerging studies are advancing genetic understanding (Delrot et al., 2020). Recent studies reported genotype-specific chloride exclusion in rootstocks as a key salinity adaptation trait, with ongoing development of functional markers (Henderson et al., 2014). For heat stress, (Leng et al., 2025) identified a SNP in *VvTTC4* linked to enhanced thermal response, potentially influencing anthocyanin biosynthesis and membrane stability.

#### 4.5 Pepper/Capsicum

New GWAS research in capsicum (2018–2024) has shown salinity-related ion transporter loci and heat-responsive genes like *CaHSP*.

Despite notable advancements, genome-wide association studies (GWAS) in horticultural crop improvement continue to face significant limitations. One key issue is the narrow crop representation (Zahid

et al., 2022). Research disproportionately focuses on a few economically important species such as tomato, potato, cucumber, and grapevine. However, many indigenous vegetables, minor fruits, and ornamentals, which often possess valuable stress-adaptive traits, are overlooked due to insufficient funding, limited genomic tools, and lack of reference genomes(Solankey et al., 2021). Expanding GWAS efforts into these underutilized crops is essential to unlock novel allelic variation for breeding climate-resilient varieties(Zenda et al., 2021a). The incredibly low coverage of tropical fruits and leafy vegetables in GWAS datasets is another gap (2010–2025 data).

Another limitation is related to sample size and phenotyping bottlenecks. GWAS requires large, genetically diverse populations and high-quality phenotypic data. Yet, many studies rely on modest panel sizes with fewer than 300 accessions, which reduces statistical power and may result in false-positive associations or missed rare alleles(Zuk et al., 2014). Additionally, phenotyping for complex traits like drought and salinity tolerance remains challenging under field conditions. A lack of standardized stress protocols and insufficient application of high-throughput phenotyping tools also hampers cross-study comparisons and meta-analyses(Reihs et al., 2025).

Moreover, most GWAS in horticulture address single stress conditions under controlled environments, which do not reflect the multifactorial stress scenarios encountered in actual field settings(Huang, 2024). Abiotic stresses such as drought, salinity, and heat often occur simultaneously or sequentially. The limited use of gene-environment interaction models further constrains the ecological relevance and breeding utility of identified loci(Des Marais et al., 2013).

## 5.2 Bioinformatics and Genetic Complexity

Many horticultural crops exhibit polyploidy and clonality, which introduce additional layers of genetic complexity in GWAS analyses. Crops such as potato and strawberry, with their complex polyploid genomes, present challenges in allele dosage estimation, homologous recombination, and interpretation of gene interactions(D'Agostino and Tripodi, 2017). Most GWAS software is optimized for diploid species, necessitating adaptations for accurate analysis in polyploids. Clonally propagated crops also exhibit extensive linkage disequilibrium due to limited recombination, leading to large haplotype blocks that complicate fine mapping and causal variant identification(Thakral et al., 2022).

Pleiotropy and genetic trade-offs are also prominent concerns in climate-resilient horticulture. A gene that enhances tolerance to drought may adversely affect traits such as fruit size or flavor(COST, 2025). While GWAS can detect pleiotropic loci, integrating this information into breeding programs is complex. Multi-trait GWAS and the incorporation of transcriptomic and metabolomic data offer potential

solutions, but they require comprehensive datasets and substantial computational resources(Farooq et al., 2024).

## 5.3 Data Accessibility and Reproducibility

Although GWAS studies often report significant SNP-trait associations, data transparency and reproducibility remain inconsistent. Essential datasets such as genotype matrices, raw phenotypic data, and summary statistics are not always deposited in open repositories(Agler et al., 2019). This hinders validation, cross-comparison, and collaborative research. Promoting FAIR data principles (Findable, Accessible, Interoperable, and Reusable) is critical for enhancing transparency in plant genomics. Furthermore, the use of standardized data ontologies and frameworks, such as those established for plant phenotyping, can facilitate interoperability and long-term data reuse(Inau et al., 2023).

## 5.4 Challenges in Underutilized and Minor Crops

Underutilized horticultural crops, often referred to as orphan crops, face a distinct set of challenges in genomics research. Many of these species lack draft genome assemblies and reliable SNP databases, limiting their utility in GWAS. Germplasm collections for minor crops are frequently small, fragmented, and poorly characterized(Xue and Cui, 2025). Inconsistent passport data and phenotypic descriptors further constrain the potential for association studies. Additionally, these crops receive limited attention and investment due to their lower market value and weaker policy support, despite their importance in local diets and resilience to harsh environments(Qureshi et al., 2015). Unlocking the potential of underutilized crops requires dedicated genomic infrastructure, expanded germplasm characterization, and integration into national and international breeding initiatives(Zafar et al., 2024).

## 5.5 The Need for Multi-Environment and Longitudinal GWAS

To improve the practical utility of GWAS findings in breeding programs, it is essential to conduct studies across multiple environments and over time. Multi-location trials across varied agroecological zones can help capture genotype-by-environment interactions and improve the robustness of trait-locus associations(Elsafy, 2025). Longitudinal phenotyping, which monitors trait development through different growth stages, enhances resolution and enables a better understanding of temporal stress responses(Wen et al., 2023). Integrating GWAS information with crop simulation models predicts trait expression under future climate conditions, allowing breeders to make informed decisions for developing climate-resilient crop varieties(Marsh et al., 2021).

## 6. Global Collaboration, Breeding Integration, and Policy Recommendations

### 6.1 The Role of International Collaboration and Shared Genomic Resources

Collaborative platforms and crop-specific genomic databases are foundational to advancing GWAS

applications in horticulture. Resources like the Sol Genomics Network and other crop-centric portals enable the use of curated genome assemblies, annotated markers, and phenotypic data ([Mansueto, 2024](#)). These materials support data harmonization, meta-analysis, and breeding decisions. There is an urgent need to improve infrastructure for underrepresented crops, particularly those critical to regional food security ([Brinkley et al., 2025](#)).

Breeding consortiums and public-private partnerships are critical for the application of GWAS findings. Projects that incorporate genotypic and phenotypic data from regional trials enable protocol standardization and rapid deployment of genomics-assisted breeding ([Lindqvist-Kreuze et al., 2024](#)). They also provide as a venue for capacity building and knowledge sharing among researchers, breeders, and industry partners. Improving these collaborations is critical for scaling up genomics. Strengthening such collaborative networks is essential to scale up genomic innovation in horticulture ([Srivastav et al., 2024](#)).

### 6.2 Translating GWAS Discoveries into Breeding Programs

The incorporation of GWAS results into breeding programs is crucial for the production of climate-resilient cultivars. Marker-assisted selection (MAS) is a technique that uses diagnostic markers derived from GWAS regions to help identify favorable variants. In contrast, genomic selection (GS) predicts breeding values by using genome-wide SNP markers in predictive models ([Sinha et al., 2023](#)). GS provides unique benefits in perennial horticulture plants with extended generation times, improving selection efficiency and speeding up growth ([Voss-Fels et al., 2019](#)).

GWAS findings also influence pre-breeding efforts, such as the introduction of resilience traits from wild relatives into elite lines. This technique improves the genetic base of modern varieties and provides access to stress-resilient alleles that are not found in the usual breeding pool ([Chen, 2024](#)). Advanced breeding procedures, such as doubled haploids and marker-assisted backcrossing, also help to effectively transmit such traits into commercial cultivars ([Hasan et al., 2015](#)).

### 6.3 Policy-Level Support for Climate-Smart Horticulture

To ensure that genetic research results may be put into reality, favorable policy conditions must exist. Genomic breeding for climate resilience should be incorporated into national agriculture and environmental policies ([Kole, 2013](#)). Investment in research infrastructure, such as germplasm banks, phenotyping facilities, and bioinformatics capabilities, is required to maintain momentum. Funding options should prioritize capacity development and the establishment of effective breeding pipelines ([Gerullis et al., 2023](#)).

In addition, policies should mandate the open sharing of genetic and phenotypic data in publicly accessible repositories. Developing optimal practices for data sharing promotes scientific integrity and worldwide innovation through collaboration ([Rehm et al., 2021](#)). Harmonization and public sector support can help to accelerate the use of genomic techniques in breeding programs, particularly in low- and middle-income countries ([Sahay, 2016](#)).

### 6.4 Future Directions for Global Collaboration

The future of climate-resilient horticulture agriculture employing GWAS can be found in a global context. Pan-genomic techniques should be utilized to incorporate structural differences and non-reference alleles, especially in genetically varied or poorly adapted crops ([Tiwari et al., 2020](#)). International benchmarking experiments can help uncover environmentally adaptable loci. New technologies, like as artificial intelligence and machine learning, have great potential for understanding complicated genotype-environment-phenotype connections, but caution must be exercised to maintain transparency and interpretability. Finally, promoting intersectoral collaboration among geneticists, agronomists, economists, and policymakers is critical ([Flanagan et al., 2018](#)).

To fully reap the benefits of GWAS research, breeding programs and studies should be connected with commercial and sustainability objectives ([Compagnucci and Spigarelli, 2018](#)). Breeding strategies and GWAS research should be integrated with market and sustainability goals to maximize the benefits of GWAS research ([Rexroad et al., 2019](#)). Between 2018 and 2024, pan-genome references for numerous crops were produced, allowing for the identification of structural changes using GWAS.

### 7. Conclusion and Strategic Recommendations

Climate change also poses threats to horticultural productivity, as it causes higher temperature swings, changes in rainfall patterns, and soil salinity ([Gora et al., 2019](#)). Genome-wide association studies (GWAS) have emerged as key techniques for understanding the genetic architecture of abiotic stress tolerance in major horticultural species including tomato, potato, cucumber, and grapevine ([Hereil, 2024](#)). Improvements in high-throughput genotyping, phenotyping infrastructure, and statistical analysis have boosted the precision of marker-trait relationships, allowing for the identification and incorporation of stress tolerance loci into breeding programs ([Tyagi et al., 2024](#)). Despite this progress, several limitations remain, particularly in underutilized species that lack genomic resources and standardized phenotyping protocols. Studies conducted between 2010 and 2024 consistently suggest that multi-environment GWAS gives the most reliable markers for climate-resilient horticulture breeding.

To accelerate progress, strategic priorities must include the expansion of GWAS into underrepresented crops, development of multi-environment phenotyping systems, and global investment in public genomic databases (Sinha et al., 2023). Additionally, breeding programs must integrate GWAS findings using genomic selection models that balance yield and stress adaptation. Strong policy support, international collaboration, and data-sharing frameworks will be essential to translate research outcomes into climate-resilient cultivars (Gaikwad). In this era of environmental uncertainty, GWAS offers a scalable and precise approach to bolster the genetic resilience of horticulture, provided it is supported by coordinated action and inclusive innovation (Hafeez et al., 2023).

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## Statements and Declarations

### Data Availability Statement

All data are fully available and can be found within the manuscript file.

### Acknowledgement

Not Applicable

### Conflicts of Interest

The authors declare no conflict of interest.

### Ethics Approval Statement

Not applicable.

### Ethics Approval Statement

Not applicable.

### Consent to Participate

Not applicable.

### Consent to Publish

Not applicable.

### Author Contributions

Conceptualization by Muhammad Hammad, Talib U, Sher A, Shafiq M, and Sherazi Shuh. Writing—original draft preparation was prepared by Hammad M; writing—review and editing was performed by Shafiq M, Talib U, Sher A. All authors have read and agreed to the published version of the manuscript.

### Funding

Not applicable.



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