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Review

Breeding and biotechnological interventions for mitigating drought in horticultural crops

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ABSTRACT

Drought is an escalating abiotic stress intensified by climate change, which is a major threat to the productivity of horticultural crops. Addressing the increasingly frequent water deficits requires shifting from generic mitigation approaches toward mechanistic understanding and targeted breeding and biotechnological interventions. This review synthesizes recent advances in drought resilience from fundamental research to field applications. At the molecular level, we analyze key genetic pathways, with the multi-omics integration and high-throughput phenotyping in trait discovery and validation. The review further discusses genomics-assisted breeding, genetic engineering and genome editing approaches that enable precise manipulation of drought-adaptive traits in horticultural crops. Complementary precision agronomic and technological interventions, when integrated with predictive modeling and precise data-driven decision-support tools, enhance the deployment and performance of drought-resilient genotypes under field conditions. We also highlight the translational research and policy initiatives as essential for overcoming socio-economic barriers for smallholder farmers. Ultimately, achieving enduring drought resilience requires the alignment of cutting-edge biotechnology with actionable policy and stakeholder-centric strategies.

Keywords: Artificial intelligence, climate resilience, drought tolerance, high-throughput phenotyping, multi-omics, transcription factors, translational research

INTRODUCTION

Horticultural crops are essential to global nutritional security, supplying essential micronutrients, vitamins, and health-promoting bioactive compounds. While historical crop improvement programs largely prioritized yield maximization under optimal environments, accelerating climate change now necessitates multidimensional strategies capable of sustaining productivity, quality and resilience under extreme weather conditions. Climate projections indicate a potential rise in mean surface temperature of up to 4.5°C by the end of 21st century (Mushtaq et al., 2024), which will intensify the frequency, duration and severity of drought stress. Among climate-induced stresses, drought represents one of the most severe constraints, contributing to annual agricultural losses exceeding USD 37 billion (https://www.fao.org/interactive/disasters-in-agriculture/en/) worldwide, largely due to the sensitivity of horticultural crops to water deficit.

Drought, characterized by a prolonged water deficit which disrupts multiple physiological and metabolic processes depending on the crop developmental stage. At the biological level, water deficit disrupts cellular homeostasis, photosynthesis, nutrient transport, and carbon metabolism while accelerating senescence. In horticultural crop species, drought impacts are often stage-specific; for example, drought stress in cucumber impairs primary root architecture and oxygen availability (Farag et al., 2019; Li et al., 2022), while in perennial fruit trees, it disrupts flowering phenology and fruit set. These physiological constraints are frequently accompanied by excessive accumulation of reactive oxygen species (ROS), leading to membrane lipid peroxidation, oxidative damage, and programmed cell death. Consequently, drought tolerance requires coordinated regulation of stress perception, signal transduction, and downstream defense responses mediated through phytohormonal signaling and transcriptional reprogramming.

Recent advances in breeding, molecular biology and biotechnology have substantially expanded opportunities to enhance drought resilience. Genome editing technologies moved beyond basic research to the targeted editing of drought-responsive regulators, including *MAPK3* (Wang et al., 2017),

NPR1 (Li et al., 2019) and *LBD40* (Liu et al., 2020) in tomato; *HyPRP1* (Tran et al., 2021) in potato enable precise modification of stress-related genes. Parallel developments in high-throughput sequencing, phenomics platforms, and multi-omics integration combining genomics, transcriptomics, proteomics, and metabolomics are accelerating precision breeding strategies. Importantly, the extensive genetic diversity conserved within horticultural germplasm collections and wild relatives provides critical reservoirs of adaptive traits for climate resilience. Introgression of beneficial loci derived from wild relatives further highlights the importance of genomics-assisted breeding approaches. Exploiting genetic diversity from wild relatives, such as the *stm9* locus in *Solanum habrochaites* (Arms et al., 2015) and *AdDjSKI* in chilli pepper (Bulle et al., 2024) is now vital for the introgression of resilient traits into commercial cultivars through genomics-assisted breeding approaches.

Although drought is a global challenge, its impacts are highly region-specific. In India, the NICRA program has identified over 100 drought-prone districts, particularly in two major tracts: (i) a semi-arid belt from Ahmedabad to Kanpur and onward to Jullundur, and (ii) the dry leeside region of the Western Ghats both receiving <750 mm of annual rainfall which threatens vast horticultural tracts (Prasad et al., 2012). Such environments expose horticultural production systems to recurring yield instability. Addressing these challenges requires identification, validation, and deployment of tolerant germplasm across diverse agro-ecological zones. However, a major bottleneck remains the translation of laboratory-based molecular discoveries into stable field performance. Horticultural crops often exhibit stage-specific sensitivity to drought stress, and complex genotype × environment (G×E) interactions frequently limit the reproducibility of controlled-environment successes under farmer field conditions. Strengthening field validation, multi-location testing, and environment-responsive breeding frameworks is therefore essential for achieving durable drought resilience.

In recent years, research has become shifting toward integrative approaches combining phenomics-assisted selection, phytohormone regulation (Liao et al., 2025), water-saving strategies (Franco-Navarro et al., 2025) and genome engineering to bridge the gap between discovery science and cultivar deployment. Translational breeding pipelines integrating genetic resources, functional genomics, and precision phenotyping are increasingly prioritized to accelerate the development of climate-resilient horticultural varieties. The present review aims to synthesize recent advances in plant response mechanisms underlying drought perception and its signaling in horticultural

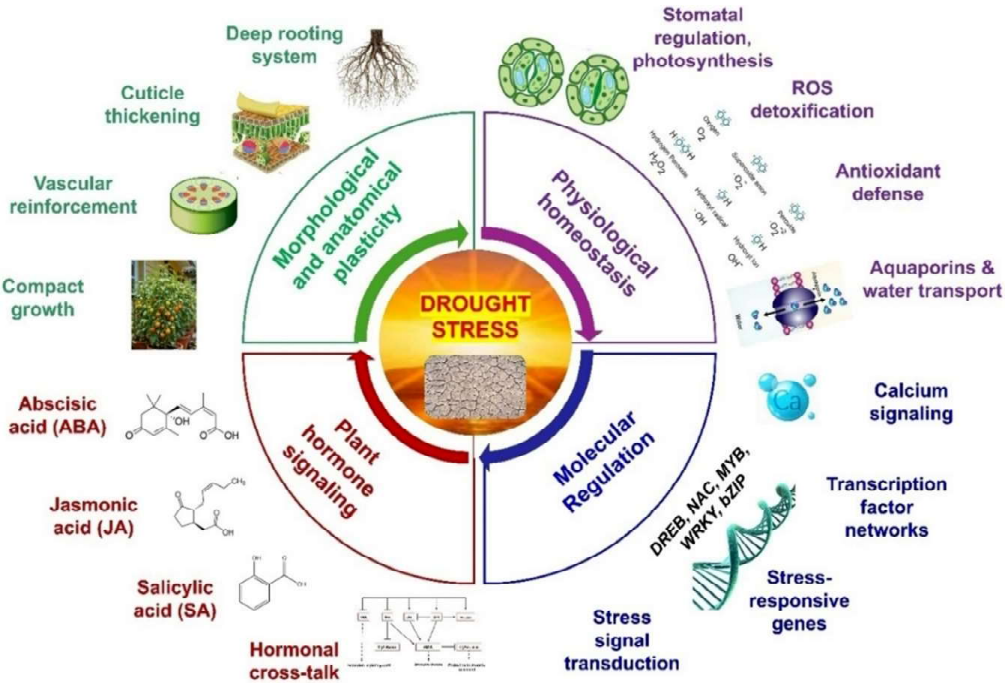

Fig. 1 : Schematic representation of the horticultural plant response to drought stress

crops, evaluate the role of genetic diversity as reservoirs of adaptive resilience traits, and outline genomics-assisted breeding and biotechnological strategies, with emphasis on lab-to-field translation for developing climate-resilient horticultural crops.

Response mechanisms of plants to drought stress

Plants withstand water deficits through interconnected morphological, physiological and molecular strategies. Stress perception initiates systemic signaling cascades that reprogram gene expression and growth dynamics, collectively shaping phenotypic plasticity in horticultural species rather than isolated adaptive responses (Fig. 1).

Morphological and anatomical plasticity

Horticultural crops exhibit diverse morphological plasticity that supports drought escape and avoidance strategies, enabling the maintenance of cellular integrity and growth under limited water availability.

Growth dynamics and escape strategies

Early responses to water deficit include the inhibition of cell expansion and mitotic activity, resulting in reduced plant height, leaf area, and overall growth (Yang et al., 2021). Drought escape is often achieved through accelerated phenological transitions. For example, the early-maturing mango 'Arka Neelachal Kesari' completes fruit set before peak summer stress (Pandey et al., 2018), while, in *Petunia* hybrid, stress-induced early flowering enhances survival (Tran et al., 2024). At the extreme, xerophytic species exhibit compact architectures that minimize exposed surface area and transpiration loss.

Integrated root-shoot and architectural modulation

Drought resilience is primarily determined by biomass partitioning and root system architecture (RSA). Traits such as deeper rooting, enhanced lateral branching, and increased root-to-shoot ratio improve water acquisition from deeper soil layers. In okra, drought tolerant genotypes (VRO 128 and VRO 160) maintain productivity by exhibiting lesser declines in root surface area and volume than sensitive types (Kumar et al., 2025). These below-ground modifications are often coupled with above-ground responses to balance the available water to plants. Leaves are sensitive to water deficit and often exhibits a reduced total surface area to minimize transpiration, while simultaneously increasing in thickness and tissue density to maintain structural integrity (Werner et al., 1999). Although such reductions in leaf expansion can lower overall photosynthetic capacity due to diminished turgor and CO_2 assimilation. The shift in biomass partitioning toward roots remains a primary survival mechanism across diverse horticultural genotypes. For example, the essential oil biosynthesis is enhanced in aromatic crops like rosemary (Bidgoli, 2018).

Anatomical adjustments and vascular integrity

At the tissue and cellular levels, plants undergo significant anatomical remodeling to minimize non-stomatal water loss and protect the hydraulic pathway. One of the most vital adaptations is the reinforcement of the leaf surface through increased cuticular thickening and epidermal wax deposition, which effectively limits residual transpiration, as observed in tea (Chen et al., 2020) and apple (Bai et al., 2019). In avocado, compact mesophyll organization with expanded palisade tissue improves water-use efficiency (WUE). Beyond the leaf lamina, the structural integrity of the vascular system is key for preventing hydraulic failure. Under water deficit, plants undergo vascular bundle plasticity characterized by increased lignification, vascular thickening and the deposition of sclerenchyma. These modifications, particularly evident in crops such as blackberry (Zhang et al., 2017), provide the necessary mechanical strength to prevent the collapse of xylem vessels and ensure the continued transport of water and nutrients during prolonged periods of drought. Importantly, these anatomical traits are exploited as stable phenotypic markers in high-throughput phenotyping and precision breeding programs.

Physiological and biochemical integration: Homeostasis under stress

The transition from water sufficiency to deficit induces coordinated physiological and biochemical reprogramming. In horticultural crops, the regulation of gas exchange, osmotic buffering, and antioxidant defense operates as an integrated network that preserves cellular integrity. While stomatal closure restricts transpiration, osmotic adjustment sustains turgor, and antioxidant systems mitigate oxidative damage associated with water limitation.

Photosynthetic constraints and photoprotective signaling

Photosynthesis is sensitive to water deficit, with net CO_2 assimilation declining due to stomatal and

non-stomatal limitations under mild stress conditions. Under severe drought, stomatal closure conserves turgor but restricts CO_2 diffusion, disrupting the electron transport chain (ETC) in photosystems I and II and leading to over-excitation. This over-excitation of the ETC triggers a 'ROS burst', including singlet oxygen ($^1O_2$), superoxide anion (O_2^-), hydrogen peroxide (H_2O_2) and the hydroxyl radical (OH), causing lipid peroxidation, protein denaturation and DNA damage. Importantly, ROS also function as signaling molecules that regulate stress perception and downstream adaptive responses (Yang et al., 2021; Haghpanah et al., 2024).

Osmotic adjustment and chaperone-osmolyte synergy

Plants accumulate compatible solutes such as proline, glycine betaine, and trehalose, which stabilize macromolecules and scavenge ROS, to sustain metabolism under low water potential. The distribution of these osmolytes is as critical as their concentration; for example, in watermelon, proline synthesized in leaves is translocated to roots to sustain water uptake and root growth under drought (Wang et al., 2022). Similarly, glycine betaine stabilizes photosynthetic and respiratory enzymes, while trehalose and other soluble sugars preserve membrane integrity and serve as rapid energy sources. A key advance is the recognition of interactions between osmolytes and late embryogenesis abundant (LEA) proteins, which act as molecular chaperones during dehydration. LEA-II proteins, enriched in lysine/glycine residues, form α-helices structures that protect enzymes and membranes (e.g. lactate dehydrogenase and β-glucosidase) and their induction by stress and ABA, e.g. dehydrin genes (*MdDHNs*) in apple (Liang et al., 2012) confirmed their protective role. Recent studies demonstrate that osmolyte-LEA complexes enhance ROS scavenging more effectively than either component alone (Renzetti et al., 2024).

Antioxidant defense and hydraulic regulation

ROS homeostasis is maintained through coordinated enzymatic and non-enzymatic antioxidant systems. Enzymatic antioxidants [superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), peroxidase (POD), glutathione peroxidase (GPX) and glutathione-S-transferase (GST)] operate alongside non-enzymatic antioxidants [ascorbate, glutathione, carotenoids, flavonoids, vitamin E and mannitol] to neutralize drought-induced oxidative stress (Haghpanah et al., 2024). Antioxidant efficiency is often genotype-specific; drought-tolerant okra genotypes VRO 128 and VRO 160 maintain higher relative water content (RWC) through elevated antioxidant activity and proline-mediated osmotic adjustment (Kumar et al., 2025). This biochemical vigor is reinforced by aquaporins (AQPs), which regulate transmembrane water transport to maintain hydraulic conductivity and cell turgor even as soil moisture depletes (Yang et al., 2021).

Water status indicators and phenological vulnerability

Leaf RWC remains a widely used indicator of plant water status and drought tolerance, including in potato (Soltys-Kalina et al., 2016). Cultivars with higher RWC, such as certain tomato (Zhu et al., 2014) and common bean (Rosales-Serna et al., 2004), often show greater drought tolerance by maintaining the 'stay-green' phenotype, which is critical for horticultural yield, as it ensures the continued remobilization of nutrients from vegetative leaves (source) to reproductive (sink), even under moisture deficit. Furthermore, water use efficiency (WUE), reflecting the balance between stomatal conductance and net photosynthesis, represents an integrative measure of water conservation. Drought impact is strongly stage-dependent, water deficit during bolting and anthesis markedly reduces seed yield in onion (El Balla et al., 2013). Some horticultural crops, such as banana, require specific assessment methods due to distinctive anatomical characteristics. Here, the rate of extension of the youngest leaf is the most sensitive and reliable indicator of water status, contrasting with less dependable traits such as leaf folding (Ravi, 2013). This highlights the need for crop-specific physiological validation to translate controlled-environment insights into field-level precision.

Molecular level responses

The above-mentioned adaptations are governed by interconnected signaling and transcriptional networks that regulate stress perception, gene expression, and downstream adaptive responses. The molecular events, involving both genetic and epigenetic regulation, operate in parallel to confer drought adaptation.

Signal perception and early signaling

Drought responses commence with stress perception and rapid signal transduction, activating divergent downstream regulatory pathways. Abscisic acid (ABA) serves as the master regulator of signal transduction, where its biosynthesis and accumulation wilting leaves trigger stomatal closure and in roots altered root architecture and the expression of drought-responsive genes. Ultimately, achieving durable resilience requires that the coexistence of ABA-independent pathways further highlights the complexity of drought signaling networks (Liu et al., 2018). Signal perception involves receptor-coupled phosphorelays, calcium (Ca^2z) fluxes and mitogen-activated protein kinase (MAPK) cascades (Yang et al., 2021). Overexpression of the osmotic stress-activated protein kinase *SRK2C* in *Arabidopsis thaliana* enhanced drought tolerance by upregulating stress-responsive genes. Moreover, drought-induced ROS act as secondary messengers that amplify stress signaling, although its signaling can be detrimental as excessive accumulation is cytotoxic. MAPK cascades, comprising MAPKKKs, MAPKKs and MAPKs transmit extracellular cues through conserved phosphorylation events, ultimately activating TFs that regulate stress-responsive gene expression (Haghpanah et al., 2024). Calcium signaling acts as a universal second messenger system in plant drought tolerance. Major calcium-sensing gene families include, Ca^{2+}-dependent protein kinases (CDPKs), calmodulin (CaM), CML and CBL proteins, which detect shifts in intracellular Ca^2z concentration and regulate the expression of drought-tolerance genes (Dekomah et al., 2022). For example, the CDPK isoform *ZoCDPK1* in

Table 1 : List of transcription factors associated with drought stress response in selected horticultural crop plants

Plant species	Transcription factors	Functional role	Level of evidence	Reference
Pepper	*CaNAC072, CaNAC104*	Differentially regulated NAC TFs involved in drought stress response; *CaNAC072* silencing enhanced drought tolerance	Virus-induced gene silencing (VIGS) functional validation	Borràs et al. (2021)
Apple	*MdNAC29*	Act as negative regulator of drought tolerance by repressing *MdDREB2A* and modulating photosynthesis and senescence-related gene expression	Transgenic overexpression; transcriptomic analysis; protein–protein and promoter interaction assay	Li et al. (2023)
Pepper	*CaATBZ1* (*bZIP TF*)	Negative regulator of ABA-mediated drought signalling regulated through ubiquitination	Loss- and gain-of-function analysis; Virus-induced gene silencing (VIGS); transgenic overexpression	Joo et al. (2019)
Chinese cabbage	*BrERF109*	Positive regulator of drought and salt stress tolerance through activation of stress-responsive genes and antioxidant enzyme activity	VIGS gene silencing; heterologous overexpression; expression profiling	Li et al. (2024)
Grapes	*VyUSPA3*	Positively regulates drought tolerance by promoting root development, ROS scavenging and ABA-related gene expression	Transgenic overexpression and RNAi silencing	Cui et al. (2023)
Chrysan-themum	*CmWRKY10*	Positive regulator of drought tolerance via ABA signalling and antioxidant enzyme regulation	Transgenic overexpression; qRT-PCR expression profiling	Jaffar et al. (2016)
Cassava	*MeWRKY20*	Regulates drought tolerance through ABA biosynthesis and H_2O_2 homeostasis as part of MeHSP90.9 chaperone complex	Protein interaction analysis; VIGS functional validation	Wei et al. (2020)

ginger regulates drought and salinity signaling, independent of DRE/CRT elements (Vivek et al., 2013), while multiple *BrrCDPK* genes in turnip are strongly upregulated under drought stress (Wang et al., 2017). Furthermore, receptor-like kinases (RLKs), characterized by extracellular, transmembrane and intracellular domains, perceive environmental signals and initiate integrated downstream signaling cascades. Under drought, RLKs activate genes associated with protective proteins and osmoprotectants, coordinate stomatal regulation via ABA crosstalk andpromote root growth to enhance access to deeper soil moisture (Sharma et al., 2023).

Transcription factors (TFs)

Following early signal perception, TFs function as key regulatory elements that translate transient signaling events into stable transcriptional reprogramming. TFs bind specific cis-acting motifs within the promoter regions of stress-responsive genes and the conserved TFs families such as DREB, NAC, MYB, WRKY, and bZIP are indispensable for orchestrating these responses (Manna et al., 2021). Among these, dehydration-responsive element binding (DREB) proteins, a subfamily of AP2/ERF (APETALA2/ Ethylene Response Factor) family, represent prominent drought regulators. DREBs bind dehydration-responsive elements (DREs) in target promoters to activate genes for root development, osmolyte accumulation, and antioxidant defense (Zhang et al., 2022). Importantly, they exhibit regulatory crosstalk with NACs and MYBs. In apple, overexpression of *MdDREB6*.2 enhanced drought tolerance by modulating endogenous cytokinin levels (Liao et al., 2017). Comparative analyses in banana further illustrate this complexity: the drought-tolerant Hill Banana (AAB) exhibits superior stomatal regulation compared to the sensitive Grand Nain (AAA), characterized by a greater reliance on DREB-independent ABA signaling pathways (Jangale et al., 2019). These findings highlight the significance of TFs and hormonal networks in shaping crop-specific drought resilience. The NAC family constitutes another major class of drought-responsive TFs, often characterized by species-specific copy number variation. Functional studies in tomato demonstrate that *SlNAC6* contributes to drought tolerance by modulating stress-responsive pathways (Jian et al., 2021). Collectively, these findings indicate that TF-mediated drought resilience emerges from integrated network-level interactions rather than single-gene dominance. A comprehensive list of TFs involved in the drought stress response in plants is furnished in Table 1.

Drought responsive genes

Drought-responsive genes encode functional proteins that directly safeguard cellular integrity and maintain water-ion homeostasis. Their induction is coordinated through TFs and hormone-mediated networks, ensuring metabolic stability under water deficit. Key classes include late embryogenesis abundant (LEA) proteins (subtypes LEA1-LEA6), dehydrins, heat shock proteins (HSPs). These act as molecular chaperones to stabilize membranes and enzymes while enhancing cellular water retention through their highly hydrophilic nature (Haghpanah et al., 2024; Şimşek et al., 2024). Simultaneously, the regulation of water and ion transport is essential to whole-plant homeostasis. Members of the aquaporin family such as PIPs, TIPs, NIPs, SIPs, and XIPs modulate transmembrane water fluxes in a tissue-specific manner. Precise regulation of plasma membrane (PIPs) and tonoplast (TIPs) aquaporins is critical for sustaining cell turgor and hydraulic conductivity, while ion transporters maintain the osmotic potential required for cellular hydration (Patel & Mishra, 2021; Sun et al., 2024).

Phytohormone regulation of drought response

Plant hormones function as regulators of drought adaptation, orchestrating a dynamic signaling network that balances growth, metabolism, and defense against abiotic stresses. Abscisic acid (ABA) serves as the primary mediator of this response, synthesized in plastids, vascular tissues, guard cells and mesophyll cells. Its biosynthesis involves the enzymatic conversion of β-carotene to ABA in the cytoplasm. It triggers stomatal closure, enhances osmotic adjustment, induces drought-responsive gene expression and promotes tap root growth into deeper soil layers during moderate drought. Ultimately, achieving durable resilience requires that its signaling extends to controlling ion homeostasis and driving metabolic adjustments essential for stress signaling (Liao et al., 2025).

Plant responses involve both ABA-dependent and ABA-independent signaling pathways, which differ primarily in their regulatory *cis*-elements,

transcriptional regulators and activation mechanisms. In the ABA-dependent pathway, drought-induced ABA accumulation binds to PYR/PYL/RCAR receptors, resulting in the inhibition of clade-A PP2C (Protein Phosphatase 2Cs), which are negative regulators of the pathway. This inhibition activates SNF1-related protein kinase 2 (SnRK2) family members, particularly group III kinases (SnRK2.2, SnRK2.3, and SnRK2.6), which play central roles in signal transduction (Fàbregas et al., 2020). Activated SnRK2s phosphorylate ABA-responsive transcription factors belonging to the AREB/ABF subgroup of basic leucine zipper (bZIP) proteins, which bind conserved ABA-responsive elements (ABREs) containing ACGT motifs within promoter regions of drought-responsive genes (Liu et al., 2018). Mutant analyses, including triple knockout lines (*SRK2D, SRK2E,* and *SRK2I*) in *Arabidopsis*, demonstrate severe ABA insensitivity, highlighting the central role of these kinases in ABA signaling (Nakashima et al., 2009). This pathway regulates osmotic adjustment, antioxidant defense, and rapid stomatal closure through ion channel activation and guard cell signaling. In contrast, ABA-independent pathways activate drought-responsive gene expression without direct ABA signaling (Liu et al., 2018). Many drought-induced genes lacking ABA responsiveness contain dehydration-responsive elements (DRE) and C-repeat (CRT) *cis*-acting elements, in their promoters, which are recognized by AP2/ERF transcription factors such as DRE-binding protein (DREB) or C-repeat-binding factor (CBF). These pathways are primarily mediated through calcium signaling, reactive oxygen species (ROS), receptor-like kinases (RLKs), and MAPK cascades, enabling rapid transcriptional responses under water deficit conditions (Wang et al., 2019). Additional transcription factors, including MYB, MYC, WRKY, and NAC families also participate in ABA-independent regulation of drought adaptation (Liu et al., 2018).

Drought responses further depend on intricate hormonal crosstalk with ethylene, salicylic acid (SA) and jasmonic acid (JA) and light-signaling pathways that refine plant adaptation (Li et al., 2023). This crosstalk is crucial for stomatal behavior and WUE. While ABA is the principal regulator of stomatal closure, its signaling is mediated by SnRK2 kinases like OST1, which activate ion channels and induce ROS and $Ca^{2}z$ oscillations in guard cells (Jalakas et al., 2018). Other hormones also contribute: BRs improve ion uptake (*SlBRI1* overexpression in tomato enhanced tolerance) (Nie et al., 2019), SA enhances the antioxidant defense system, JAs contribute by enlarging root surface area, and SLs regulate stomatal closure (Liao et al., 2025).

Finally, ABA integrates with other hormones like GA to manage seed dormancy, germination and drought escape strategies, ensuring reproductive success (Sano & Marion-Poll, 2021). Insights from these diverse hormones signaling pathways provide a framework for marker-assisted breeding and ongoing crop improvement programs for enhanced drought resilience.

Morpho-anatomical plasticity includes compact growth to limit transpiration, deeper root systems for enhanced water uptake, and increased lignification to preserve hydraulic stability. Physiological regulation involves stomatal control to balance gas exchange and activation of antioxidant enzymes to mitigate ROS-induced damage, while aquaporins maintain cellular water balance and turgor. At the molecular level, drought triggers calcium signaling, activate transcription factors and inducing stress-responsive genes such as dehydrins and LEA proteins. These processes are coordinated through phytohormonal crosstalk, with ABA as the central regulator interacting with JA and SA to enhance phenotypic plasticity and drought survival.

Breeding and biotechnological approaches for drought resilience

Drought tolerance is a polygenic trait and conventional breeding has been constrained by dependence on phenotypic selection, low heritability of key traits, and strong genotype x environment interactions. Recent advancements have shifted towards using genomics-assisted breeding (GAB) that integrates molecular tools, genomics, multi-omics analyses, and computational models with precise phenotyping to more efficiently develop drought-tolerant crops (Şimşek et al., 2024).

Genetic screening and identification of drought tolerant germplasm

Identification of drought-tolerant germplasm is the primary step in developing resilient horticultural crops. Screening approaches commonly integrate physiological and morphological traits such as stomatal conductance, transpiration rate, relative water

content and root system architecture, evaluated under controlled conditions or drought-prone environments to ensure stability. For example, drought-tolerant cucumber genotypes were identified at the germination stage using 18% PEG 8000 during seed germination (Anonymous, ICAR-IIHR, 2025). Similar screening efforts across horticultural crops have highlighted the importance of combining controlled assays with field validation. Identified tolerant sources, including cultivated varieties and wild relatives, serve as valuable donors for direct cultivation or for the introgression of drought-resilience traits through breeding and biotechnological approaches.

Horticultural crops exhibit considerable variation in drought endurance linked to phenology, ecology and genomic constitution. Early-maturing varieties can escape terminal drought by completing sensitive stages before soil moisture depletion. Several underutilized fruit crops naturally adapted to arid and semi-arid regions, such as *bael*, *kair*, *karonda*, wood apple, custard apple, *jharber*, *khejri*, *khirni*, aonla, jamun, Manila tamarind, *pilu* and *timroo* are important drought-resilient crops (Meena et al., 2022). In extremely dry zones, ber cultivars like gola, seb, and mundia are recommended, while in dry regions, banarasikadaka, kaithli, umran, and maharwali perform well (Sharma et al., 2013). Genomic composition also influences drought response, as banana genotypes containing the 'B' genome (AAB) show greater drought tolerance than 'A' genome types due to improved water-use efficiency (Ravi 2013). A comprehensive and updated catalog of drought-tolerant germplasm across horticultural crops is detailed in Supplementary Tables 1 and Table 3 of Sharma et al. (2013).

Drought-resistant plant varieties are often exchanged globally to enhance agricultural resilience. In India, the ICAR-National Bureau of Plant Genetic Resources (NBPGR) facilitates these exchanges. Notable introductions include *Gladiolus dalenii* (EC 1099553) from South Africa; drought-resistant wild rose species such as *Rosa hemisphaerica*, *R. moschata*, *R. roxburghii*, *R. woodsii*, *R. carolina*, *R. palustris* and *R. virginiana* from the USA; *Moringa stenopetala* accessions (EC1077611–1077615) from Kenya; an almond hybrid (EC1160666, USA-SG1 Titan) and apple accessions (EC971990–971991) from USA; and potato varieties such as Camel, El Mundo, Everest, and AFP08-59 (EC959700, EC959701, EC959702, EC959703) from the Holland.

Genomics-assisted breeding and molecular tools

Genomics-assisted breeding accelerates drought-resilience improvement by enabling the selection of superior genotypes using molecular markers tightly linked to target genes or quantitative trait loci (QTLs). Marker systems such as AFLP, SSRs and SNPs, have been widely used to dissect drought-responsive traits and facilitate precise selection. However, conventional QTL mapping based on biparental populations remains challenging in many horticultural crops, particularly fruit trees, due to long juvenile phases, high heterozygosity and frequent polyploidy. To overcome these constraints, association mapping, particularly genome-wide association studies (GWAS), has emerged as a powerful alternative by exploiting historical recombination events within diverse germplasm collections, thereby improving mapping resolution. This approach has been successfully applied in crops such as, okra (Ahmad et al., 2022), potato (Alvarez-Morezuelas et al., 2023), faba bean (Gutiérrez et al., 2023) and Persian walnut (Arab et al., 2022), to identify markers associated with drought-tolerance traits. A summary of reported markers and their associated drought-responsive traits across horticultural species is provided in Table 2.

Although GWAS has substantially advanced marker–trait discovery, its effectiveness is often constrained by a reliance on single-nucleotide polymorphisms (SNPs) and a single reference genome, which may not fully capture population-level genomic diversity. To address this limitation, k-mer-based GWAS (alignment-free association mapping) has emerged as a reference-independent approach capable of simultaneously detecting SNPs, structural variants, and presence–absence polymorphisms. By utilizing short fixed-length nucleotide sequences (k-mers) rather than a linear reference genome, this strategy enables the identification of complex genomic regions frequently missed by conventional methods, which is particularly advantageous for highly heterozygous and polyploid horticultural genomes. Despite these advantages, k-mer mapping introduces challenges related to computational demand and downstream biological interpretation. Future priorities therefore include workflow standardization and the development of user-friendly analytical platforms capable of linking

Table 2 : Molecular markers associated with drought-tolerance traits in horticultural crops

Crop	Gene/Marker	Linked trait/Gene	Reference
Banana	*MaPIP1;1*	Aquaporin activity	Xu et al. (2014)
Apple	*MdDREB2A*	Enhanced drought tolerance via gene expression regulation	Lian et al. (2021)
Cassava	*MeSCL30*	Metabolism	Weng et al. (2021)
Potato	*StRFP2*	Protein turnover	Qi et al. (2020)
Potato	*StDREB1, StERF3*	Root development under waterDeficit	Çelik (2024)
Okra	*Unigene10673, Unigene99547, Unigene152901, Unigene129684*	Relative water content	Ahmad et al. (2022)
Tomato	*SlARF4*	Stomatal closure and RWC regulation	Bouzroud et al. (2020)
Tomato	*SlWHY2*	Mitochondrial function & ROS scavenging	Meng et al. (2020)
Tomato	*SlProT1/2*	Proline accumulation & osmotic adjustment	Akbudak & Filiz (2020)
Tomato	*SlALMT15*	Regulates stomatal development	Ye et al. (2021)

significant k-mers to functional genomic variation. Once key markers are identified and functionally validated, they can be used in molecular breeding strategies like marker-assisted selection (MAS), marker-assisted backcrossing (MABC), gene pyramiding, and genomic selection (GS) to accelerate the development of drought-resilient horticultural cultivars.

Genetic engineering and genome editing approaches

Genetic engineering and genome editing are vital for enhancing drought tolerance when natural genetic variability is insufficient. Techniques like RNA interference (RNAi) have elucidated gene functions, such as the *CsATAF1*-RNAi cucumber plants showed reduced tolerance, whereas *CsATAF1* overexpression enhanced drought resilience (Wang et al., 2018). Furthermore, engineering of ABA receptor variants, such as PYR1, has improved drought tolerance in transgenic *Arabidopsis* and tomato by allowing inducible stress responses via agrochemical activation (Park et al., 2015).

Early transgenic methods established proof-of-concept by targeting specific signaling, metabolic pathways andthe biosynthesis of osmoprotectants. Tomato transformed with abacterial *mannitol-1-phosphate dehydrogenase* (*mtl*D) gene exhibited enhanced tolerance to drought and salinity (Khare et al., 2010). Similarly, overexpression of TFs such as AtDREB1 and BcZAT12 in tomato cv. H-88 showed drought tolerance through enhanced antioxidant activity (Krishna et al., 2021), while bspA expression in tomato cv. Pusa Ruby conferred improved drought adaptation (Roy et al., 2006). But transgenic methods are constrained by regulatory concerns and the risk of pleiotropic effects or unpredictable gene expression.

To overcome these barriers, genome editing, base editing and epigenetic modifications are gaining prominence. Advancements in CRISPR/Cas9 genome editing have allowed precise modifications for improved drought tolerance, exemplified by gene knockouts in tomato. Ultimately, achieving durable resilience requires that the knockout of *ALD1*, *FMO1*, *Solyc11g044840* and *Solyc07g04243* in cv. 'Condine Red' improved drought resilience in tomato (Wang et al., 2021), while targeted disruption of *LBD40* in the 'Micro-Tom' cultivar enhanced drought tolerance (Liu et al., 2020). Other methods, like Virus-Induced Gene Silencing (VIGS), use virus vectors to target plant mRNAs, aiding in gene function studies. For example, the knockdown of the drought-inducible variant H1-S in tomato has resulted in increased drought tolerance and enhanced stomatal closure (Şimşek et al., 2024). Together, these advances illustrate how the integration of functional genomics, gene editing, and molecular breeding is rapidly reshaping the landscape of drought-resilient horticultural crop development.

Integrated multi-omics and predictive modeling for precision breeding

A comprehensive understanding of the plant response to drought is essential for effective strategy development, achievable through multi-omics integration. While genomics and transcriptomics identify drought-responsive genes and regulatory elements; proteomics assesses changes in signal transduction and metabolic pathways; and metabolomics highlights stress-associated molecules for osmo protection and cellular homeostasis. Ultimately, achieving durable yields requires that this holistic view facilitates the identification of molecular targets for breeding climate-resilient cultivars. Advanced analytical methods utilizing machine learning and AI-driven models further enable the prediction of molecular responses with high precision. For example, generalized computational models developed aim to enhance the identification of abiotic stress-responsive microRNAs (miRNAs), as exemplified by databases like BlackP2MSATDb (Black Pepper Polymorphic Microsatellite Database; ICAR-IASRI, 2023) and the 'ASmiR' online prediction server (Pradhan et al*.,* 2023).

Predictive modeling also evaluates the broader environmental context of drought. Recent studies reveal that diminished soil moisture from monsoon failures intensifies land surface heating, thereby exacerbating drought severity. Analyses of multi-source datasets confirmed a strong land-atmosphere coupling in India, where soil moisture loss following droughts increasesthe likelihood of summer heating. Integrating such environmental datasets with plant response models provides an advanced framework for drought forecasting and management. By combining multi-omics insights with high-throughput phenotyping and AI-based predictive models, precision breeding pipelines can be developed, accelerating the creation of drought-resilient cultivars while improving proactive management strategies.

High-throughput phenotyping (HTP) and speed breeding

High-throughput phenotyping (HTP) or phenomics, has transformed drought-resilience breeding by enabling automated, precise and non-destructive evaluation of complex traits, overcoming the limitations of conventional phenotyping. HTP platforms like phenospex range from ground-based systems to unmanned aerial vehicles (UAVs) equipped with multispectral and thermal imaging sensors, allowing the rapid assessment of drought-responsive indicators such as stomatal conductance, leaf rolling and canopy temperature (Yang et al*.,* 2020). While field phenotyping remains the ultimate determinant of yield performance under stress, controlled environments enable the uniform imposition of drought at specific developmental stages; often utilizing specialized tools like track-mounted trolleys. Combining these approaches ensures that trait evaluation is both robust and physiologically relevant.

A diverse array of imaging technologies now drives HTP accuracy. They are as follows: (i) Canopy temperature (CT)/IR thermography serves as an integrative measure of plant water status, linked to stomatal conductance and WUE. Reduced evaporative cooling under drought increases leaf and canopy temperature, detectable with infrared thermometers or thermal cameras. Thermal imaging provides spatially resolved maps for large-scale genotype screening, though trait expression requires standardized environmental conditions for reliable assessment (Prashar & Jones, 2014). Complementing this, (ii) Near-infrared (NIR) and short-wave infrared (SW-IR) imaging detect leaf hydration changes by measuring water absorption bands (1450-1550 nm) and reduced absorption directly correlate with reduced evaporative cooling. Systems like those from Lemna Tec provide quantitative data on drought across different time scales. (iii) Spectral reflectance and stress imposition techniques are field based evaluations that employ canopy spectral reflectance (Gutierrez et al., 2010), line-source irrigation, withholding irrigation, salinity stress, and hotspot trials to identify drought tolerant genotypes. (iv) Chlorophyll fluorescence provides insight into photosynthetic efficiency and evaluates stress-induced limitations on light capture and energy transfer. Furthermore, these remote sensing tools, when integrated with field-based semi-automated platforms and barcode recognition systems, allow for large-scale, cost-effective genotype screening.

Beyond trait identification, speed breeding has emerged as a pivotal strategy to shorten generation times and accelerate variety development. By optimizing growth conditions or modifying flowering time, speed breeding facilitates rapid cycling without the regulatory hurdles of transgenic methods, as demonstrated in crops such as amaranth (Stetter et al., 2016). Ultimately,

achieving durable resilience requires that the integration of precision-controlled measurements with advanced imaging and speed breeding creates a high-efficiency pipeline for capturing both the physiological basis and real-world expression of drought tolerance.

Rhizosphere-mediated resilience and precision agronomic enablers for drought mitigation

The rhizosphere is shaped by root exudates that drive biological communication, enhancing plant growth and drought resilience. Drought restructures the plant microbiome, preferentially enriching monoderm (Gram-positive) over diderm (Gram-negative) bacteria (Naylor & Coleman-Derr, 2018). Beneficial microorganisms, including arbuscular mycorrhizal fungi and plant growth-promoting bacteria, alleviate drought stress through direct mechanisms such as phytohormone synthesis and the indirect suppression of stress-induced ethylene. Exopolysaccharide production promotes biofilm formation and improves soil water retention. Plants selectively recruit beneficial microbes while restricting pathogens via immune components such as pattern recognition receptors (PRRs) and nucleotide-binding leucine-rich repeat (NLR) proteins. Drought modifies immune signalling, potentially facilitating beneficial root colonization. Altered SA and JA pathways under drought influence microbiome assembly, leading to selective enrichment of drought-tolerant endophytes in the root zone, consistent with the 'cry for help' hypothesis. Dissecting plant–microbe–drought interactions require integrated meta-omics approaches. Synthetic Communities (SynComs) enable the controlled reconstruction of plant–microbiome interactions, linking plant molecular responses with microbial ecology to elucidate community assembly and stress adaptation mechanisms (Ait-El-Mokhtar et al., 2023).

Beyond rhizosphere-mediated resilience, precision agronomic and technological interventions are critical for mitigating drought stress and improving water-use efficiency (WUE). As water scarcity intensifies, the emphasis shifts from yield per unit area to yield per unit water. Effective strategies include optimized planting dates, balanced fertilizer application to promote deeper rooting, and mulching to reduce evaporation. Ultimately, achieving durable yields requires that integrated practices, such as mulch combined with deficit irrigation, are effective in crops such as pomegranate and Aonla under challenging environments. Advances in irrigation technologies, including drip irrigation and micro-sprinklers, minimize evaporative losses and enable targeted water delivery. Deficit irrigation and partial root-zone drying enhance water-use efficiency while maintaining crop quality in tomato and potato. Its signaling and the integration of real-time monitoring using sensors and remote technologies further strengthens this framework, supporting sustainable productivity under increasing drought stress (Samreen et al., 2023).

Translational research: from lab to field – successes and hurdles

Translating scientific discoveries into practical solutions for drought-stressed agricultural systems is essential for climate resilience; however, this process is hindered by technological gaps, socio-economic barriers, and challenges in adoption. India has made significant progress, particularly through the establishment of the ICAR-National Institute of Abiotic Stress Management (NIASM) in 2009, which addresses abiotic stresses responsible for up to 50% of yield losses. The ICAR-NIASM mandate encompasses crops, livestock, and fisheries, serving as

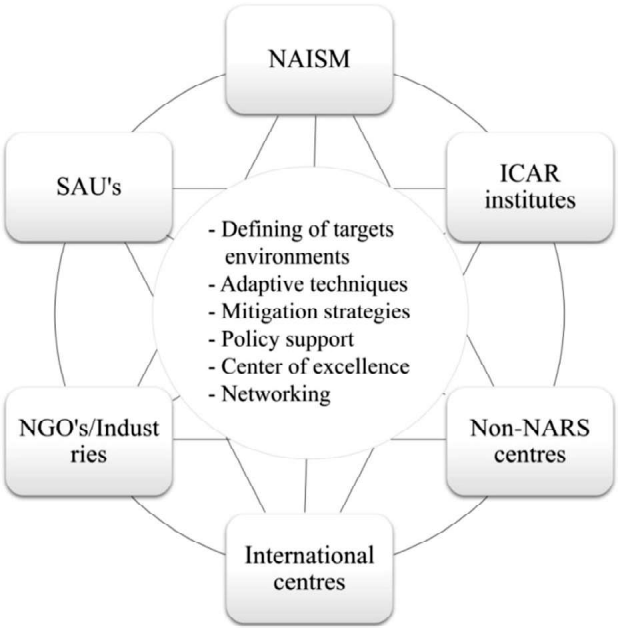

Fig. 2 : A six-point strategy adopted by the National Institute of Abiotic Stress Management to enhance the efficiency and effectiveness of research endeavors. SAU's-State Agricultural Universities, NGO's-non-governmental organizations, ICAR-Indian Council of Agricultural Research, NARS-National Agricultural Research System

a national repository for stress management information and promoting advanced research, training, and policy development aimed at climate-smart agriculture.To fulfil these objectives, NIASM implements a six-point interlinked strategy (Fig. 2) that includes environment-specific research, innovative technology, and collaboration. Under its Vision-2050 initiative, NIASM focuses on integrating plant phenomics, hyperspectral remote sensing, and crop simulation models to manage water stress effectively. This framework aids in molecular studies of stress responses and facilitates the development of climate-resilient horticultural varieties (http://niam.res.in/sites/default/files/pdfs/NIAM_Vision-2050.pdf).

Complementing these institutional efforts are advanced monitoring and decision-support systems. The South Asia Drought Monitoring System (SADMS) was developed by the International Water Management Institute (IWMI) in collaboration with ICAR, itutilizes remote sensing and satellite data to provide regional-level drought forecasts and real-time weather updates. The system's scalability is demonstrated by its adaptation into the Zambia Drought Management System (ZADMS). While SADMS provides a robust regional foundation for tracking drought severity through satellite-based vegetation and soil moisture indicators, its macro-level monitoring traditionally lacked direct field connectivity. To bridge this gap, innovative digital tools like the Sukha Rakshak AI (Drought Protector) platform emerged as an integrated, AI-powered drought intelligence system (Amarnath et al., 2025). Sukha Rakshak AI represents a paradigm shift from reactive relief to proactive resilience by utilizing Retrieval-Augmented Generation (RAG) and vector databases to synthesize data from SADMS, Google Earth Engine, and localized contingency plans. This architecture enables the generation of hyper-local, predictive advisories that answer specific farmer queries, such as crop-shifting strategies during delayed monsoons. To ensure inclusivity, the system integrates AI4Bharat and Sarvam models, delivering multimodal (text and voice) advisories in over 22 Indian languages. By linking global monitoring infrastructure with localized, actionable intelligence, this framework empowers stakeholders to anticipate and adapt to moisture-scarce environments effectively. The global relevance of this framework was highlighted at the United Nations' AI for Global Good Summit (July 8, 2025). Following this, the system entered a rigorous phase of fine-tuning for agricultural extension agencies, government officials, and drought managers. This is being followed by pilot deployments in Odisha and Tamil Nadu (August 2025) to validate its localized, actionable intelligence before broader introduction to the farming community (https://www.iwmi.org/blogs/india-to-get-its-first-ai-based-chatbot-to-tackle-drought/).

Sustained drought resilience ultimately depends on the development of crop varieties capable of maintaining yield stability under both optimal and water-limited environments. This requires integrating genomics-assisted breeding with multi-environment field validation to capture genotype × environment (G×E) interactions influencing trait expression. Approaches such as genomic selection, speed breeding, and high-throughput phenotyping enable simultaneous selection for productivity and stress adaptation. Incorporation of resilient germplasm through marker-assisted introgression further enhances adaptive plasticity without compromising yield potential. Importantly, phenomics platforms, remote sensing tools, and crop simulation models now allow breeders to evaluate water-use efficiency, root architecture, and canopy responses under realistic field conditions. Strengthening participatory breeding, multi-location trials, and climate-resilient testing networks will therefore be critical to translating molecular discoveries into farmer-ready horticultural varieties capable of sustaining productivity across variable moisture environments.

Future perspectives

Building climate-smart horticultural systems requires strong policy support and global collaboration to tackle drought-related challenges. The Integrated Drought Management Programme (IDMP), created by the WMO and GWP, enhances national drought policies through early warning systems, vulnerability assessments, and mitigation strategies. The International Drought Resilience Alliance (IDRA) promotes worldwide drought preparedness, recognizing drought as a socio-economic crisis. A 'people-centred approach' is essential for aligning global goals with local action. Institutions like ICAR-NIASM in India advance abiotic stress management through technologies and eco-specific strategies, while AI-driven decision-support platforms exemplify the merging of science with governance. The transition to

ecosystem-based solutions is critical for overcoming socio-economic and institutional barriers and for bolstering horticultural resilience against severe droughts.

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