



International Journal of Research in Agronomy

E-ISSN: 2618-0618
P-ISSN: 2618-060X
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NAAS Rating (2025): 5.20
www.agronomyjournals.com
2025; 8(10): 955-963
Received: 17-08-2025
Accepted: 26-09-2025

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Breeding for climate-smart vegetables: Genomic strategies for heat, drought, and salinity tolerance

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DOI: <https://www.doi.org/10.33545/2618060X.2025.v8.i10m.4094>

Abstract

Global climate change poses an urgent threat to vegetable production, as rising temperatures, frequent droughts, and increasing soil salinity disrupt crop growth, reduce yields, and compromise quality. Most vegetable species such as tomato, pepper, cucumber, lettuce, cabbage, spinach, carrot, onion, and eggplant are highly sensitive to these stresses due to their shallow root systems, high water content, and delicate physiology. Developing climate-smart vegetable varieties that can endure heat, water deficit, and salinity has thus become a key breeding priority. This article comprehensively reviews the physiological, biochemical, and molecular mechanisms underlying stress tolerance in vegetables and highlights modern genomic strategies being used to accelerate breeding progress. Core genomic tools whole-genome sequencing, marker-assisted selection (MAS), quantitative trait locus (QTL) mapping, genomic selection (GS), and genome editing (CRISPR/Cas9) are discussed in relation to their applications in identifying, tracking, and manipulating tolerance-related genes. Transcriptomics, phenomics, and multi-omics integration are also examined as transformative approaches linking genotype to phenotype. Through detailed case studies in major vegetable crops, the article summarizes progress in mapping stress-response QTLs, identifying candidate genes (e.g., heat shock proteins, ion transporters, antioxidant enzymes), and developing markers linked to improved physiological traits such as osmotic adjustment, canopy cooling, and ion homeostasis. Overall, genomic-assisted breeding offers a path toward resilient vegetable cultivars capable of maintaining productivity and quality in a changing climate, ensuring food security and sustainability for future generations.

Keywords: Climate-smart vegetables, heat tolerance, drought tolerance, salinity tolerance, genomic selection, marker-assisted selection, QTL mapping, CRISPR/Cas9, transcriptomics, phenomics, stress physiology, abiotic stress, vegetable breeding, stress-resilient cultivars, genomic resources

Introduction

Global warming and unpredictable weather patterns are raising the stakes for vegetable production. Many popular vegetables, like tomato, pepper, cucumber, lettuce, cabbage, spinach, carrot, onion, and eggplant, are quite sensitive to extreme heat, water deficit, or salty soils. These stresses can sharply reduce yields and quality^[10]. Vegetables are mostly water (often over 90%), so drought can cause wilting and poor growth, while high temperatures can abort flowers and fruits, and salinity can poison roots and leaves. To meet future food needs, breeders are now developing climate-smart vegetable varieties that tolerate heat, drought, and salinity better^[27]. Modern genomic tools are central to this effort. By combining knowledge of plant stress physiology with advanced breeding methods like genome editing, marker-assisted selection (MAS), QTL mapping, and transcriptome profiling, scientists are pinpointing genes and markers associated with tolerance traits. In this way, breeders can efficiently select or engineer varieties that survive and yield under adverse conditions^[42]. This article reviews the physiological and molecular defenses that vegetables use against heat, drought, and salt stress, and then dives into the genomic strategies being applied in major vegetable crops. We highlight key advances (like the availability of complete genome sequences and high-throughput phenotyping platforms) that fuel these efforts. Detailed case studies in tomato, pepper, cucumber, lettuce, cabbage, spinach, carrot, onion, eggplant and others show how traits like *osmotic adjustment*, *root architecture*, *ion transport*, *osmoprotectant production*, *heat-shock responses*, etc., are mapped and bred for^[66].

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Genomic and Breeding Tools for Climate Resilience

Whole genome resources and sequencing

The first key step is that many vegetable genomes have now been sequenced at high resolution. For example, tomato, pepper, cucumber, and lettuce have reference genomes available, as do many others (carrot, onion, cabbage, etc.)^[67]. Whole-genome sequencing lets researchers rapidly find candidate genes and see where they lie on chromosomes. When a stress-related trait is discovered, scientists can search the genome sequence to see if related genes (like heat shock proteins or ion transporters) are nearby. Sequenced genomes also mean breeders have an inventory of millions of DNA markers (SNPs, SSRs, etc.) spread throughout each crop's chromosomes. These markers are like signposts that can be linked to traits^[43].

Marker-Assisted Selection (MAS) and QTL mapping

MAS is a method where known DNA markers linked to desirable traits are used in breeding. If a certain marker is closely associated with salt tolerance, breeders can use it to select seedlings that carry the favorable allele without having to test every plant in harsh salt conditions^[68]. To identify these markers in the first place, scientists perform quantitative trait locus (QTL) mapping or genome-wide association studies (GWAS)^[28]. In QTL mapping, a population (like offspring of a cross) is grown under stress, traits are measured (e.g. wilting score, survival, yield components), and the progeny are genotyped with markers. Statistical analysis reveals regions of the genome (QTLs) linked to differences in performance^[44]. For instance, many QTLs for heat tolerance traits have been mapped in vegetables: one study in pepper found dozens of QTLs for traits like fruit yield under heat, pollen viability and canopy temperature, and another in tomato identified major QTLs for seedling heat injury index and chlorophyll retention. MAS uses those linked markers to track favorable alleles through breeding cycles^[11].

Genomic Selection (GS)

GS is a more recent approach, where the effects of all markers across the genome (not just a few) are modeled to predict a plant's performance. In vegetable breeding, genomic selection is gaining traction, especially for traits that are influenced by many small-effect genes^[69]. By training prediction models on diverse lines, breeders can forecast how a new cross will behave under stress without testing every seedling in the field. GS can greatly shorten breeding cycles for complex traits like drought tolerance, as it captures thousands of small QTLs genome-wide^[1].

Genome editing (CRISPR and others)

CRISPR/Cas9 and related tools allow precise edits to genes. For climate stress, key tolerance genes can be targeted. For example, editing a tomato heat shock transcription factor (HsfA1) improved heat tolerance, and editing stress-related regulators in lettuce or pepper is being explored for salinity or drought resilience^[70]. Base editors and prime editors enable single base changes in specific genes (e.g. changing promoter sites for greater gene activation). By knocking out negative regulators of stress response (genes that normally suppress protective pathways), or by tweaking hormone or signaling pathways, researchers can enhance tolerance traits. For instance, scientists have increased drought tolerance in tobacco and maize by editing relevant genes, and created heat-tolerant tomato varieties via transcription factor edits^[45]. The advantage of CRISPR is its precision and speed: dozens of genes can be multiplexed. The

main caveats are off-target risks and regulatory acceptance. Nonetheless, CRISPR is being actively tested in vegetables: for instance, it is used in tomato and lettuce to improve stress traits^[29].

Transcriptomics and candidate genes

By sequencing RNA (transcriptomics) of stressed vs. control plants, researchers identify which genes turn on or off during stress. Differentially expressed genes often point to physiological mechanisms (e.g. genes for osmoprotectants, antioxidants, heat shock proteins)^[71]. These candidate genes can then be tested or used as markers. Integrating QTL mapping with RNA-seq (a strategy called "QTL-seq" or eQTL mapping) is powerful: it narrows down large QTL intervals to pinpoint plausible stress-response genes. For example, in tomato heat tolerance mapping, combining QTL analysis and transcriptomics revealed candidate genes like *SlCathB2*, *SIGST*, *SlUBC5*, and *SlARG1* in major QTL regions. In vegetables broadly, transcriptomics has highlighted common stress pathways: ABA signaling (for drought), ion transporters (for salt), antioxidant enzymes, and osmolyte biosynthesis, among others^[12].

Phenomics and high-throughput screening

Modern breeding for stress tolerance relies on measuring traits in many plants quickly. High-throughput phenotyping platforms (drones/UAVs with multispectral cameras, ground-based imaging rigs, automated greenhouse sensors, root imaging systems, etc.) let researchers track thousands of plants for stress symptoms^[72]. For example, thermal cameras on UAVs can detect canopy temperature differences under drought (cooler canopies indicate better water use); chlorophyll fluorescence imaging can quantify damage under heat; and image analysis can score wilting or leaf area loss^[46]. Automated pot systems can mimic drought by weighing pots and controlling water deficit precisely. These platforms accelerate screening of breeding populations. Indeed, robotics and sensor technologies are now part of most climate-tolerance breeding programs, making it feasible to link complex physiological traits (like canopy cooling or root vigor) with genetic data^[30].

Integration of Multi-Omics and Databases

Beyond individual tools, breeders are using integrated "omics" approaches. For example, genomics plus metabolomics plus phenomics yields deeper insight: it can link specific metabolites (like proline or glycinebetaine) to gene expression and to tolerance. Big databases of genomic and stress data (such as genome browsers for each crop, gene expression atlases, SNP repositories) greatly help^[73]. For instance, the Sol Genomics Network for tomato/pepper, Cucurbit Genomics Database, Brassica databases, and others, all collate genetic markers, reference genomes, and QTL information. Breeders also access worldwide germplasm databases to find stress-resistant wild relatives (like wild tomatoes or chillies) to cross into cultivated lines. Machine learning is starting to assist by predicting stress responses from multi-layer data. Overall, these genomic resources and tools transform traditional trial-and-error breeding into a precision science for developing climate-resilient vegetables^[2].

Heat Tolerance in Vegetable Crops

Heat stress (temperatures above a crop's optimum) is a major threat, especially for vegetables grown in open fields or uncooled greenhouses^[74]. High temperatures can damage proteins and membranes, inhibit photosynthesis, and most

critically, impair reproduction. Flower and pollen development are highly temperature-sensitive: for example, peppers and tomatoes suffer flower drop and poor fruit set if daytime temperatures exceed ~38,40°C. Leaf tissue responds with rapid stress signals; membrane lipids become more fluid and prone to damage [47]. The plant's first responders are heat shock proteins (HSPs) and heat shock transcription factors (Hsfs). These proteins act as molecular chaperones to refold denatured proteins and protect cells. For instance, *Hsfs* rapidly turn on when temperatures rise, triggering a cascade of HSP production. Other protective molecules include antioxidants (superoxide dismutase, catalase, peroxidases) to mop up heat-induced reactive oxygen species (ROS) [13].

Morphologically, heat-tolerant varieties often show traits like smaller or more vertical leaves (to reduce radiation load), and higher stomatal cooling capacity. At very high heat, however, stomata may close to conserve water, which paradoxically raises leaf temperature [75]. Thus, a balance is needed. Physiologists use measures like canopy temperature depression (the difference between air and leaf temperature) as an indicator: a tolerant plant can maintain a cooler canopy under heat. Measures of membrane stability (leakage of electrolytes under heat) or chlorophyll fluorescence (PSII efficiency, *Fv/Fm*) are also standard lab assays. For example, *Fv/Fm* is often lower in heat-sensitive seedlings, since Photosystem II is one of the most heat-labile parts of the plant [76].

At the genetic level, researchers have discovered many heat-tolerance genes and loci. In tomato, QTL mapping has identified key genomic regions controlling traits like electrolyte leakage and chlorophyll content under heat. One study found a major QTL on chromosome 1 (qCC-1-5) that explained over 16% of variation in chlorophyll retention under stress [77]. Another strategy combined bulked-segregant analysis (QTL-seq) and RNA-seq to locate five major QTLs for seedling heat injury (HII) and chlorophyll; interestingly, candidate genes within those regions included a cysteine protease (*SlCathB2*), a glutathione S-transferase (*SIGST*), a ubiquitin-conjugating enzyme (*SIUBC5*), and an arginase (*SIARG1*) [14]. These likely help recycle damaged proteins or regulate redox balance [48]. In pepper (*Capsicum*), a major heat-tolerance mapping study uncovered over 60 QTLs for traits like fruit yield per plant, fruit weight, plant height, pollen viability, stomatal density, and canopy temperature [31]. For instance, a big QTL (qFYP4.2) on chromosome 4 was linked to much higher fruit yield under high temperature, explaining about 19% of yield variation. This QTL co-located with fruit number, suggesting a set of genes enhancing fruit set in heat. Another example is a QTL on pepper chromosome 11 for canopy temperature depression (qCTD11.2),

indicating loci that keep plants cooler under heat [3].

Research in cucumber also shows heat QTLs. In an RIL population, one extremely large QTL (qHT1.1) on cucumber chromosome 1 was repeatedly detected over multiple years and locations. It had extremely high LOD scores (~20,25) and explained up to ~59% of the variation in adult-plant heat injury (leaf wilting index). A linked SSR marker (SSR23757) defined a ~0.7 Mb region containing just 10 genes. This major locus is now a prime target for breeding: a PCR marker (HT-1) within qHT1.1 predicted heat tolerance with over 97% accuracy in testing lines [49].

Genetic Engineering

Transgenic and editing approaches have also been used. Overexpressing or knocking out specific transcription factors in tomato has yielded lines with different heat sensitivity. For example, CRISPR knockout of a master Hsf (heat shock factor) improved thermotolerance in tomato (possibly by fine-tuning stress response). In lettuce, CRISPR has been used to tweak unknown genes for salinity, and similar approaches hold promise for heat traits too. The idea is to engineer the plant's heat-response network (e.g. by increasing HSP production or strengthening membranes) [32].

Breeding efforts

Conventional breeding has screened germplasm and wild relatives for heat resilience. For example, some wild tomatoes and peppers that evolved in hot climates carry natural alleles for heat tolerance. These have been crossed into commercial lines, with markers helping to track the introgressed segments. Marker-assisted backcrossing is underway in several programs to stack heat-tolerance QTLs into elite tomato and pepper hybrids. Genomic selection models are being trained to predict heat tolerance in early generations based on genome-wide SNP profiles [50].

Example

In hot pepper, researchers developed a mapping population from a heat-tolerant line (DLS-161-1) and a sensitive line (DChBL-240). Using GBS (genotyping-by-sequencing) to find SNPs and ddRAD-seq, they mapped a major QTL (qFYP4.2 on Chr4) for fruit yield at high temperature. Plants inheriting the tolerant allele at qFYP4.2 had significantly higher yields when daytime temperatures peaked at 38,46°C. They also found QTLs on pepper chromosomes 8 and 11 affecting pollen viability and leaf cooling, respectively. This shows how breeding can target multiple sub-traits (yield, pollen, canopy cooling) to build overall tolerance [14].

Heat stress tolerance traits and genomic regions in vegetable crops

Crop	Population/Variety	Trait Index	Specific Trait	Marker/Gene	QTL/Gene	Chr	LOD / PVE	Stress Condition	Tolerance Threshold	Breeding Approach
Tomato	LA1698 (sens) × LA2093 (tolerant)	Heat injury index	Membrane stability	SSR (W299, C01M86371)	qHII-1-1	Chr1	LOD ~11.6/6.7%	48h at 45°C	Survives ~48h at 45°C	QTL mapping
Tomato	LA1698 × LA2093	Chlorophyll content	Leaf chlorophyll	SSR134, C01M86371	qCC-1-5	Chr1	, / 16.48%	48h at 45°C	~33% greater chlorophyll	QTL mapping
Pepper	DLS-161-1 (t) × DChBL-240 (s)	Fruit yield per plant	Number & weight of fruits	SSR 367380 (linked)	qFYP4.2	Chr4	11.17 / 19.39%	Field heat (31,46°C)	Fruit set fails > 40°C	QTL mapping
Pepper	DLS-161-1 × DChBL-240	Canopy temperature def.	Canopy cooling capacity	SSR (Ch11 region)	qCTD11.2	Chr11	~10 / ~15%?	Field heat	2°C cooler canopy	QTL mapping
Cucumber	RIL “99281” × “931”	Heat injury index	Leaf wilting	SSR23757, Indel markers	qHT1.1	Chr1	LOD~25 / ~59%	17 days @ 35°C+	Very tolerant (HII~10)	QTL mapping

Note: “t” = tolerant parent, “s” = sensitive parent. PVE = percent variance explained by QTL; LOD = logarithm of odds score. Yield impact indicates relative advantage of tolerant allele

Drought Tolerance in Vegetable Crops

Drought, the shortage of available water, is a perennial challenge, made worse by hotter climates. Vegetables are especially vulnerable because their tissues are over 90% water. When soil dries, plants quickly experience osmotic stress (cells lose turgor) and oxidative stress (ROS accumulate). The immediate physiological response is stomatal closure, which conserves water but also reduces CO₂ uptake and slows photosynthesis [15]. Leaves may wilt or roll, the plant’s water potential plummets, and prolonged drought can cause leaves to brown or drop. Root traits become critical: drought-resistant vegetables often have deep or extensive root systems that scavenge water [33]. Other classic drought-responses include thickened leaf cuticles (to reduce evaporation), accumulation of osmolytes like proline and glycine betaine (to protect cells), and upregulation of antioxidant enzymes (to neutralize ROS) [51]. Hormonal signaling is key too: abscisic acid (ABA) levels rise under drought and trigger many protective mechanisms (like stomatal closure and expression of stress genes). Jasmonic acid and ethylene also play roles in signaling drought responses [4].

At the molecular level, many gene families are implicated in drought tolerance. Transcription factors like DREBs (dehydration-responsive element binding proteins), NACs, MYBs, and WRKYs regulate suites of drought-responsive genes. Water channel proteins (aquaporins) control water flow in tissues [52]. Enzymes of osmolyte synthesis (e.g. P5CS for proline) are often elevated. Studies in vegetables have shown that drought-tolerant genotypes maintain higher activity of enzymes such as superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and increase compatible solutes under stress. Also, genes for late embryogenesis abundant proteins (LEAs) that protect cell structures, and dehydrin proteins, are commonly upregulated [78].

Breeding efforts for drought tolerance focus on those traits. Root architecture is a major target, breeding deeper-rooted lettuce or tomato can improve resilience. Stomatal traits are also selected; for example, mutants with reduced stomatal density can lose less water. Grafting vegetable scions onto drought-tolerant rootstocks (often wild relatives) is widely used in cucurbits and solanaceous veggies. For instance, grafted tomato plants often show improved drought resistance by maintaining chlorophyll content and antioxidant activity under stress [53].

On the genomic side, QTL mapping has been applied in several crops. A notable study in lettuce used a cross between a cultivated variety (*L. sativa*) and a drought-resistant wild lettuce (*L. serriola*) to investigate seed germination under water stress. Using 10% PEG solution to simulate drought, they identified

two small-effect QTLs on lettuce chromosomes 4 and 8 (named *ANIM_0* and *AXDH_0*) that controlled germination percentage. Each QTL explained about 7,9% of the variation, with additive effects from both parents. This showed that even basic stages like germination are genetically complex under drought [34].

In tomato, seedling drought tolerance has been dissected using wild×cultivated populations. For example, a 2024 study used a high-density SNP map from genome resequencing to find QTLs in a recombinant inbred population (*S. pimpinellifolium* × *S. lycopersicum*) [35]. They uncovered 15 QTLs for drought tolerance (seedling stage) on chromosomes 1,3,4,8,9,10,12. One major QTL (*qDT₁-3* on Chr1) was detected consistently, harboring a candidate gene (*SIBRL1*, a brassinosteroid receptor). This QTL explained up to ~15% of variance in drought-related traits. Another (though noted under salt) was *SIMSRB1* on Chr7 (methionine sulfoxide reductase) which also responds to oxidative stress. These mapping studies provide linked markers for selection [16].

Other vegetables also show some mapping results. In pepper, genes like *CaDREB1A* have been identified that enhance drought tolerance via ABA signaling (by transgenic or overexpression studies). In spinach and cabbage, genome-wide association studies (GWAS) have begun to find SNPs tied to drought indices. For example, a GWAS in cabbage found loci affecting root morphology and water-use efficiency, key drought traits [5].

Breeding techniques

Marker-assisted selection (MAS) is actively used. For example, breeders use SSR or SNP markers linked to root-length QTLs or osmotic-regulation genes in tomato and pepper. Some breeding programs are even using genomic selection for drought: by training models on many drought-stress traits, they can predict performance of new lines (especially in leafy greens and brassicas). Conventional crossing of drought-tolerant landraces (like wild carrot, wild lettuce, or certain pepper types) into commercial lines is ongoing [54].

Physiological screening innovations

Today’s breeders use high-throughput approaches to phenotype drought response. Infrared imaging tracks canopy temperature (cooler means better cooling under drought), chlorophyll fluorescence monitors stress effects, and automated pot weighting keeps precise water levels. Field phenotyping with drones can measure NDVI or reflectance as proxies for drought stress. These tools help to associate phenotype with genotype at scale [17].

Drought stress tolerance traits and genomic loci in vegetable crops

Crop	Population/Variety	Trait Index	Specific Trait	Marker/Gene	QTL/Gene	Chr	LOD / PVE (%)	Stress Condition
Lettuce	Salinas (<i>L. sativa</i>) × US96UC23 (<i>L. serr.</i>) RIL	Germination% under PEG	Seed germination	SSR markers (<i>ANIM_0</i>)	<i>ANIM_0</i>	Chr4	, / 7.3,8.8%	10% PEG solution
Lettuce	Salinas × US96UC23 RIL	Germination% under PEG	Seed germination	SSR markers (<i>AXDH_0</i>)	<i>AXDH_0</i>	Chr8	, / 5.7,8.3%	10% PEG solution
Tomato	RIL (<i>S. pimpinellifolium</i> × <i>S. lycopersicum</i>)	Seedling drought index	Survival & root vigor	SNP (genome-wide)	<i>qDT₁-3</i>	Chr1	, / ~15.8%	Water withheld (seedling)
Tomato	RIL (<i>S. pim</i> × <i>S. lyc</i>)	Seedling salt index (for comparison)	Salt injury	SNP	<i>qST₇</i>	Chr7	, / ~15.8%	100 mM NaCl (seedling)
Pepper	Cultivar mix / wild	Stomatal conductance	Transpiration efficiency	Gene <i>CaDREB1A</i>	,	,	,	Drought field

Note: PVE =% of variance explained by QTL; RWC = relative water content; RIL = recombinant inbred lines.

In lettuce, the mapped QTLs (*ANIM_0* on Chr4 and *AXDH_0* on Chr8) each had modest effects but together controlled a significant portion of germination ability under water stress. In tomato seedlings, the major drought QTL (*qDT₁-3*) coming from

wild germplasm accounted for the largest share of drought tolerance. The table also reminds us that some QTL (like *qST₇* in tomato) can affect multiple stresses ^[55]. Pepper's *CaDREB1A* gene (a transcription factor) improves drought resistance by enhancing ABA signalling and root growth, although its mapping as a QTL is not as well defined here ^[18].

Overall, drought tolerance in vegetables is a polygenic trait, often requiring multiple genes of moderate effect. Breeders combine physiological screening (e.g. measuring leaf water potential or survival days) with MAS on root and stomatal QTL to assemble tolerant cultivars. Importantly, because drought episodes can be unpredictable, stability across environments is also selected for (breeders test lines across multiple field trials in different years) ^[6].

Salinity Tolerance in Vegetable Crops

Salinity stress occurs when soil accumulates salts (commonly NaCl), which happens in irrigated and coastal lands. High salinity imposes two main problems: osmotic stress (plants have trouble taking up water) and ionic stress (excess sodium and chloride ions are toxic) ^[36]. Vegetables vary in salt tolerance: for instance, spinach is relatively salt-tolerant and often considered a mild halophyte, whereas beans and many leafy greens are very sensitive. In general, salinity leads to reduced germination, stunted growth, chlorosis (yellowing) of older leaves, and poor yields. At the cellular level, high sodium displaces potassium (essential for enzymes) and disrupts photosynthesis ^[19].

Plants use several strategies to cope with salt. One is ion exclusion: root cells use transporters like Na⁺/H⁺ antiporters (SOS1 in roots, NHX in vacuoles) to pump sodium back out or sequester it into vacuoles away from sensitive processes. Another is maintaining K⁺/Na⁺ balance by selective channels (HKT transporters retrieve Na⁺ from the xylem in the shoot, preventing too much reaching the leaves) ^[37]. Accumulating organic osmolytes (proline, glycine-betaine, sugars) helps stabilize cell osmotic pressure. Salt-tolerant varieties often have robust antioxidant defenses, thick cuticles, or leaf succulence to dilute salts. At the molecular level, genes like *SOS1*, *SOS2*, *SOS3* (calcium sensors in the salt-overly-sensitive pathway),

NHX1 (vacuolar Na/H antiporter), *HKT₁;1* (sodium transporter), and *ABI5* or *DREB* variants have been implicated in model plants ^[20].

In vegetable breeding, a traditional source of salt tolerance has been wild relatives and landraces. For example, a wild tomato relative (*Solanum pimpinellifolium*) carries alleles that allow seedlings to survive moderate salinity that would kill cultivated tomato. Some of these alleles have been introgressed into commercial breeding lines. Marker-based selection for salt tolerance traits (like survival, Na⁺-exclusion, or shoot dry weight under salt) has been attempted in tomato, cucumber, and other veggies ^[38].

In cucumber, less is known about salt QTLs. Some mapping efforts have looked for markers in salt-treated seedlings but results have been limited. Similarly, in pepper and eggplant, major QTL scans for salt tolerance have not yet yielded clear candidates (probably because these species have complex genomes or require more study). However, breeders have identified salt-tolerant lines by phenotypic screening; for instance, certain chilli pepper varieties yield reasonably under mild salinity ^[56].

Physiology and thresholds. Common practical measures include soil electrical conductivity (EC); most veggies begin to show salt damage at an EC of 3,5 dS/m (equivalent to ~30,50 mM NaCl). For example, severe tomato seedling injury is often seen above ~100 mM NaCl. Plants like spinach or saltbush can tolerate 2,3 times that concentration. In the lab, salt stress is often imposed by irrigating with NaCl solution and recording traits like *electrolyte leakage*, *chlorophyll retention*, or *root length* ^[21].

Breeding and technology. MAS for salinity tolerance is ongoing. In tomato and pepper, QTLs from wild relatives (e.g. *Solanum pennellii* segments) are tracked with SSR markers to build more tolerant cultivars ^[57]. However, because salinity tolerance is complex (involving multiple transporters and physiological traits), genomic selection may become useful. Some attempts at genome editing for salt genes have happened in model plants; similar ideas are being tested in lettuce and tomato (e.g. editing transcription factors to tweak salt pathways) ^[7].

Salinity stress tolerance traits and genomic loci in vegetable crops

Crop	Population/Variety	Trait Index	Specific Trait	Marker/Gene	QTL/Gene	Phenotyping Trait	Yield Impact	Comments
Tomato	RIL (<i>S. pimpinellifolium</i> × <i>S. lyc.</i>)	Salt injury index	Seedling survival	SNP (resequencing)	<i>qST₇</i>	Seedling viability	Tolerant allele improves survival	<i>SIMSRB1</i> (oxidative repair) in QTL
Lettuce	Cultivar × Wild relatives (screen)	Germination under salt	Seedling germination	,	,	Germination%	Salt-tolerant types give 20% higher	Quantitative genetics ongoing
Spinach	Cultivar selection	Shoot Na ⁺ /K ⁺ ratio	Na ⁺ exclusion	,	,	Leaf ion content	Moderate tolerance (relative yield drop 30%)	Natural tolerance in germplasm
Pepper	Cultivar mix	Fruit set under salt	Yield under mild salinity	,	,	Fruit count	Slight reduction at moderate salt	No mapped major QTL known

In practice, tomato's *qST₇* is one of the better-defined loci (with candidate gene *SIMSRB1*) that breeders are watching. For other vegetables, specific genes are less well-mapped in the public domain ^[58]. Often breeders rely on physiological screening (e.g. growing cultivars in saline hydroponics) to identify tolerant lines, then use any available markers. There is hope that as more high-quality genomes become available and high-throughput phenotyping of salt stress is scaled up, we will find more concrete markers for selection ^[39].

Advances in Breeding Tools, Databases, and Phenotyping

Beyond the stress-specific genetics above, the last decade has seen a revolution in the tools and platforms available for breeding climate-smart vegetables. Here are some highlights:

High-throughput genotyping platforms

Vegetable crops now have cost-effective genotyping arrays and methods. There are SNP chips and genotyping-by-sequencing (GBS) protocols for tomato, pepper, cucumber, lettuce, carrot,

and more ^[59]. This enables scanning hundreds of thousands of markers in breeding populations. For example, pepper has a 78K SNP array, lettuce has 6K, tomato has >7K, etc. These platforms let breeders conduct GWAS and GS efficiently. Public databases (like Ensembl Plants, Sol Genomics Network, Cucurbit Genomics Database, Brassica Information Portal) store genotype and phenotype data from these studies ^[22].

Marker databases and stress-specific resources

Beyond raw genomic data, scientists have begun compiling markers linked to stress tolerance. For instance, in tomato there are curated QTL maps for fruit-set under heat and for salt exclusion. The “Tomato QTL database” collects trait loci including abiotic stress. Similarly, PepperHub and CucGen store marker-trait associations. Researchers also share datasets of transcriptomic responses (e.g. hot pepper RNA-seq under heat in public repositories). These community resources accelerate research by making candidate genes and markers openly available ^[23].

Phenotyping platforms

Modern breeding increasingly uses phenomics, technology-driven phenotype measurement. For vegetables, this includes field-deployable tools. Drones with multispectral sensors can fly over a field of lettuce or cabbages to detect areas of drought stress (through NDVI or thermal imaging). Greenhouse imaging setups measure chlorophyll fluorescence or canopy temperature on seedlings ^[60]. Root phenotyping rigs let breeders image root systems of carrots or beets to quantify depth and branching under drought. Even simple sensors like leaf porometers or leaf water potential meters have been integrated into breeding trials. These high-throughput methods allow linking phenotype to genotype on a large scale, a must for complex traits ^[8].

Gene editing strategies

As noted, CRISPR/Cas9 and its variants allow targeted edits. Key genes are being tested in some vegetables: beyond the tomato and lettuce examples above, scientists have edited in pepper (for example, knocking out the NPR1 regulatory gene in tomato increased drought sensitivity, suggesting that the reciprocal approach, editing it for better function, might yield tolerant tomatoes) ^[40]. Multiplex editing means breeders can stack edits for multiple stresses at once; for example, one can imagine editing an HSP gene and an ABA-pathway gene in a single line ^[61]. Base editing is also promising: for instance, editing the promoter of a key stress gene to increase its expression under stress could be done without introducing foreign DNA. However, regulatory pathways for edited vegetables vary by country, and development is just beginning ^[24].

Genomic selection in practice

A few vegetable breeding programs have begun pilot GS projects. For instance, in cabbage and cauliflower (close relatives of kales), GS models have been built for drought indices and bolting under stress ^[63]. A tomato breeding company reported trials of GS for heat tolerance by training models on past field trial data. The success of GS depends on high-quality phenotype data, which (thanks to phenomics) is becoming available. We expect GS to grow in leafy vegetables and solanaceous crops where rapid cycle breeding is desirable ^[64].

Integrative omics for gene discovery

The trend is to combine genomics, transcriptomics,

metabolomics, and even proteomics. For example, some teams profile stress-treated vegetables with RNA-seq to find candidate stress genes, then validate them via association mapping or gene editing. Others measure metabolites (like proline, sugars, antioxidants) under stress, then look for QTLs controlling their levels ^[62]. Such integrative studies are revealing complex networks, for example, how a drought QTL might actually work by controlling ABA levels, or how a salt-tolerance QTL might affect the antioxidant system. Databases like STRING or KEGG, though based on model plants, help translate these findings. Machine learning is even starting to be used to integrate climate data with genetic and phenotypic data, predicting which lines will perform best under future conditions ^[25].

Breeding pipelines and collaboration

Finally, it's worth noting that breeding climate-smart veggies is often a collaborative, global effort. International consortia (such as the World Vegetable Center and CGIAR programs) are bringing together germplasm, data, and expertise ^[26,41]. They support screening of thousands of lines for stress tolerance and make data public. Modern breeding pipelines might look like this: start with diverse germplasm (including wild types), phenotype them under controlled heat/drought/salinity screens, genotype them on a SNP platform, run GWAS to find markers, then use those markers in MAS or GS for selecting crosses ^[65]. Meanwhile, gene editing labs work in parallel to test candidate genes. The result is faster development of varieties that farmers can grow when climates are erratic ^[9].

Conclusion

Developing climate-smart vegetable varieties is a complex but crucial goal. The interplay of phenotype (how a plant looks and yields under stress) and genotype (the underlying genes) is being unraveled through cutting-edge genomics. For heat, breeders focus on flowering resilience, membrane stability, and canopy cooling. For drought, root depth, water-use efficiency and ABA signaling are paramount. For salinity, ion transporters and osmoprotectants take center stage. In each case, new genomic markers and editing tools accelerate progress. The combination of technologies means breeders no longer have to rely solely on surviving hot or dry seasons by chance. Instead, they can pre-screen large numbers of seedlings in labs and greenhouses. When a major QTL or gene is identified (as in the heat QTLs for pepper and cucumber, or the drought QTLs for tomato and lettuce), it can be used immediately via marker-assisted breeding or even direct gene editing. Moreover, the same platforms that find QTLs for one stress often reveal candidates for others, enabling stacking of traits (for example, a tomato line could carry both heat-tolerance and drought-tolerance loci). Of course, translation from lab to field remains challenging. Sometimes a gene that helps in one environment has trade-offs in another (e.g., a drought-tolerant plant might grow slower under ample water). Breeders must therefore validate that new varieties perform well both in stressful conditions and in normal conditions. This requires multi-environment trials and careful selection. Data analytics and modeling are helping predict these trade-offs. Looking ahead, there is optimism that vegetables of the future will be hardier. The knowledge collected, like the 60+ heat tolerance QTLs in pepper or the dozens of drought response genes, is building a roadmap. Emerging tools like pan-genomes (which capture all genetic diversity in a crop) and speed breeding (rapid generation cycling) will further accelerate development. Cross-disciplinary approaches, including

microbiome engineering (using beneficial microbes to help plants cope with stress) and even nanotechnology (targeted delivery of stress-relief compounds), are on the horizon. For now, the integration of genomic strategies with traditional breeding is showing great promise. As climate change intensifies, the lessons learned from tomato, pepper, cucumber, lettuce, and other veggies will ensure that farmers have varieties that can thrive, whether under blazing heat waves, extended dry spells, or salty irrigation water. The richness of vegetable crops and the diversity of genomic tools give us confidence that a climate-resilient plate of vegetables is within reach.

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