International Journal of Plant & Soil Science

Volume 38, Issue 9, Page 16-35, 2026; Article no.IJPSS.164528
ISSN: 2320-7035

CRISPR-Cas9 Precision Breeding for Climate-resilient Vegetable Crops: A Critical Appraisal of Evidence, Inference and Deployment

Manisha A. Kharat [a++], Vaibhav U. Bansod [b++*], Nisha R. Thorat [b++], Shreya P. Wasre [b#], Dhanshree M. Birkad [b#] and Shriram B. Mahale [b#]

[a] Department of Horticulture, College of Agriculture, Vasantrao Naik Marathwada Krishi Vidyapeeth, Parbhani, Maharashtra, India.
[b] Department of Vegetable Science, Dr. Panjabrao Deshmukh Krishi Vidyapeeth, Akola, Maharashtra, India.

Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

Article Information

DOI: https://doi.org/10.9734/ijpss/2026/v38i96264

Open Peer Review History:
This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: https://pr.sdiarticle5.com/review-history/164528

Review Article

Received: 23/06/2026
Accepted: 12/08/2026
Published: 14/08/2026

Abstract

Vegetable crops occupy a small share of global cropland yet supply a disproportionate fraction of dietary micronutrients, and their short life cycles, high water demand and thermosensitive reproductive stages make them unusually exposed to a warming and more variable climate. Clustered regularly interspaced short palindromic repeats and CRISPR-associated protein 9 (CRISPR-Cas9) editing has been promoted as a route to climate-resilient vegetable cultivars, and the descriptive literature cataloguing edited targets has expanded quickly. This critical narrative review evaluates whether that literature supports the resilience claims made for it. Peer-reviewed studies published between January 2015 and June 2026 were identified through

[++] Ph.D. Scholar; [#] M.Sc. Student;
**Corresponding author: E-mail: vaibhavbansod111@gmail.com;*

Cite as: *Kharat, M. A., Bansod, V. U., Thorat, N. R., Wasre, S. P., Birkad, D. M., & Mahale, S. B. (2026). CRISPR-Cas9 Precision Breeding for Climate-resilient Vegetable Crops: A Critical Appraisal of Evidence, Inference and Deployment. International Journal of Plant & Soil Science, 38(9), 16–35. https://doi.org/10.9734/ijpss/2026/v38i96264*

openly accessible bibliographic indexes and citation-metadata services, appraised for design adequacy, evaluation environment and evidence-claim alignment, and synthesised thematically rather than catalogued. Three findings dominate. First, the evidence base is heavily weighted towards single-gene loss-of-function alleles created in a small number of transformation-competent model genotypes, assessed under controlled conditions using physiological proxies rather than marketable yield, so that demonstrated gene function is repeatedly reported in language implying demonstrated agronomic improvement. Second, several loci yield directionally opposite phenotypes depending on the stress applied, which indicates that stress-specific reactive oxygen species thresholds and pleiotropy are poorly resolved and that resilience cannot be treated as a single transferable trait. Third, the small number of studies that combine allele-resolution editing of regulatory sequence with field evaluation and yield endpoints produce markedly stronger inference than the knockout literature, suggesting that the principal constraint is experimental design and delivery capability rather than nuclease performance. Regulatory divergence, patent uncertainty and uneven transformation capacity across vegetable species further separate laboratory demonstration from field deployment. Confidence in current claims of climate resilience remains low for most targets, and progress will depend on multi-environment field testing, yield-based endpoints, and extension of editing capability beyond the few genotypes that presently regenerate reliably.

Keywords: *Genome editing; abiotic stress tolerance; horticultural crops; prime editing; cis-regulatory alleles; plant regeneration; agricultural biotechnology policy.*

1. Introduction

Vegetables account for a modest proportion of harvested area worldwide but contribute a large share of dietary vitamins, minerals and phytochemicals, and their nutritional value depends on physiological processes that are strongly temperature and water dependent. Modelling of environmental change effects on horticultural production indicates that increases in mean temperature, reductions in water availability and rising tropospheric ozone are associated with lower yields of vegetables and legumes and with declines in the nutritional quality of harvested tissue, with the projected losses concentrated in regions that already have low vegetable intake (Scheelbeek et al., 2018). Physiological analyses reach compatible conclusions from a different direction, identifying reproductive development, tissue water status and postharvest quality as the components of vegetable production most sensitive to warming and to greater climatic variability (Bisbis et al., 2018). Climate change also reshapes the biotic environment, altering pathogen geography, overwintering success and epidemic timing in ways that place additional pressure on cultivars selected under earlier conditions (Miller et al., 2024).

Conventional breeding has responded to these pressures, but the traits concerned are difficult. Reproductive thermotolerance in tomato (*Solanum lycopersicum* L.) is polygenic, and quantitative trait locus (QTL) analyses across diverse germplasm resolve many loci of small effect whose expression depends on the evaluation environment (Bineau et al., 2021). Combined QTL mapping, bulked-segregant sequencing and transcriptome analysis in the same species identify heat-tolerance intervals that contain large numbers of candidate genes and that have not been converted into deployed cultivars at the rate the underlying urgency would justify (Wen et al., 2019). Pyramiding several small-effect alleles by recurrent selection is slow in crops with long inbreeding requirements and is complicated further by linkage drag when donors are wild relatives.

Site-directed nucleases were introduced into this context as a way of creating defined alleles without prolonged crossing. The system based on CRISPR-Cas9 rapidly became dominant because of the ease with which guide RNAs can be designed, and vegetable species, particularly within the Solanaceae, became early testbeds. Editing of the *CLAVATA3* promoter in tomato generated a graded series of alleles affecting locule number and fruit size, demonstrating that quantitative variation could be engineered directly rather than sought in existing germplasm (Rodríguez-Leal et al., 2017). Two groups independently edited domestication and improvement loci in wild tomato relatives to produce plants combining stress-associated wild backgrounds with cultivated architecture and fruit traits (T. Li et al., 2018; Zsögön et al., 2018). Comparable work in the orphan Solanaceous species *Physalis pruinosa* L. altered plant architecture and fruit size within a single generation (Lemmon et al., 2018), and editing of flowering and shoot-architecture genes produced determinate, early-harvest tomato and groundcherry ideotypes intended for controlled-environment production (Kwon et al., 2020). These studies established that precise allelic change is technically achievable in horticultural Solanaceae and framed the expectation that climate-resilience traits would follow. A recent review of plant genome engineering describes a CRISPR-Cas toolkit that includes engineered Cas variants as well as base and prime editing, thereby broadening the range of sequence changes accessible for crop research and breeding (Tuncel et al., 2025). In tomato, use of a GRF-GIF morphogenic regulator has also improved regeneration and recovery of edited plants, underscoring regeneration efficiency as a practical determinant of genome-editing throughput (Swinnen et al., 2025).

The reviews that have accompanied this expansion are numerous and largely convergent in structure. Surveys of genome editing in vegetable crops enumerate edited species, target genes and reported phenotypes, and conclude that the technology holds substantial promise (Kim et al., 2021; Devi et al., 2022; Das et al., 2023; Sood et al., 2025). Reviews focused on abiotic stress list candidate targets for drought and salinity across crop groups and describe the tools available for modifying them (Shelake et al., 2022), while species-focused syntheses do the same for *Brassica* crops (Ton et al., 2025). A recent mechanistic review of heat tolerance in vegetables assembles the signalling and transcriptional networks underlying thermotolerance and identifies breeding strategies that could exploit them (Y. Li et al., 2026). These contributions are useful as maps of activity. They rarely ask, though, whether the primary studies they compile actually establish improved performance under field conditions relevant to climate adaptation, whether the reported phenotypes are internally consistent, or whether the inferential distance between a physiological proxy measured on potted plants and marketable yield under heat stress has been bridged. Where directionally contradictory results exist for the same locus, catalogue reviews tend to report both without reconciling them. A 2026 synthesis of climate-resilient horticultural crops

likewise identifies transformation constraints and gaps in field translation as continuing limitations for applied genome-editing strategies (Wu et al., 2026).

That omission matters because the applied claim and the experimental warrant have diverged. A substantial share of the primary literature consists of reverse-genetic experiments in which a candidate gene is knocked out and the mutant is compared with the wild type under an imposed stress, using membrane-damage, reactive oxygen species (ROS) and antioxidant-enzyme measurements as endpoints. Such experiments are appropriate for establishing gene function. They do not, on their own, establish that the edited allele would improve yield stability in a commercial genotype grown in a variable field environment, and several of them report reduced rather than improved stress tolerance in the mutant. Reading the resulting corpus as a pipeline of climate-resilient cultivars overstates what has been demonstrated.

1.1 Scope, Research Gap and Objectives

This review is bounded to the use of CRISPR-Cas9 and its catalytically modified derivatives, including cytosine and adenine base editors and prime editors, for the creation of defined alleles in vegetable crops, with the primary focus on traits relevant to climate resilience. Vegetable crops are taken to include fruit vegetables and tuber crops of the Solanaceae, cucurbit vegetables, cole and leafy Brassicaceae, and leafy Asteraceae. Traits considered relevant to climate resilience comprise tolerance of high temperature, water deficit, salinity and chilling, reproductive stability under thermal stress, and resistance to pathogens whose epidemiology is being altered by warming. The technical, agronomic, regulatory and social dimensions of deployment are treated as part of the same problem rather than as an appendix.

The gap addressed is evidential rather than descriptive. Existing reviews document which genes have been edited in which species; they do not systematically appraise the strength of the inference connecting those edits to climate resilience, nor do they examine why apparently similar experiments yield opposite conclusions. No prior synthesis has taken the evaluation environment, the phenotypic endpoint, the genetic background and the control design as the organising axes of appraisal across the vegetable editing literature, or asked what would have to change methodologically for the field to generate claims that plant breeders and regulators could act upon.

Several adjacent areas are excluded. Transgenic approaches that introduce foreign coding sequence, RNA interference strategies, epigenome editing without sequence change, editing of cereals, oilseeds and fibre crops, editing of fruit trees and ornamentals, and applications of CRISPR-derived systems to pathogen diagnostics rather than plant improvement all fall outside the scope. Postharvest quality traits are considered only where they interact directly with climate exposure.
Five objectives follow. The first is to characterise the editing modalities in use and the range of allelic variation each can access in vegetable species. The second is to appraise, theme by theme, the evidence that edited alleles confer tolerance of heat, water deficit, salinity and chilling, distinguishing demonstrated gene function from demonstrated agronomic improvement. The third is to analyse directionally inconsistent findings and their probable causes rather than reporting them side by side. The fourth is to identify the methodological features that most limit inference across the corpus and to assess whether recent work has begun to remedy them. The fifth is to set out research priorities that are specific enough to be actionable, together with the governance and access conditions that would determine whether laboratory results reach growers.

2. Methods for Literature Selection

2.1 Review Design and Rationale

A critical narrative review was selected in preference to a systematic review, scoping review or meta-analysis because the review question concerns the quality and coherence of an evidence base rather than the magnitude of a defined effect. The primary literature is heterogeneous in species, target locus, stress protocol, growth environment and phenotypic endpoint to a degree that precludes meaningful quantitative pooling; no two studies of tomato thermotolerance, for example, apply the same temperature regime, duration, developmental stage and measurement set. Typologies of review methodology identify the critical review as the appropriate form when the objective is to evaluate and interpret a body of work and to produce a conceptual contribution rather than an exhaustive enumeration (Grant & Booth, 2009). Narrative synthesis retains the interpretive latitude needed to compare incommensurable designs and to reason about why results diverge, a capability that rigidly protocolised approaches sacrifice (Greenhalgh et al., 2018; Sukhera, 2022).

Narrative design does not license opacity. The Scale for the Assessment of Narrative Review Articles specifies that a defensible narrative review must justify its importance, state its aim, describe its literature search, present evidence in support of its statements, and refer appropriately to the strength of that evidence (Baethge et al., 2019). Those requirements were adopted as working standards. Search sources, search strings, eligibility rules and appraisal criteria are reported below; every substantive claim is attributed to a source whose bibliographic identity was verified; and the confidence attaching to each conclusion is stated explicitly in the synthesis rather than left implicit.

2.2 Information Sources

Literature was identified through Europe PMC, which indexes MEDLINE and PubMed records together with full-text open-access life-science content, and through the Crossref Metadata Search interface, which was used both for discovery and for bibliographic verification. General web searching of institutional and organisational websites supplemented these indexes for policy and

regulatory material. Backward citation searching from recent reviews and forward tracing of highly cited primary studies were used to locate work that keyword searching missed, and targeted checks were made for corrections, expressions of concern and retractions attaching to candidate sources.

Subscription-restricted indexes, including Web of Science Core Collection, Scopus and CAB Abstracts, were not accessible during the preparation of this review, and no search of those resources was performed. An attempt to query the OpenAlex scholarly index returned an access restriction and yielded no usable records. The coverage of this review is therefore bounded by what the accessible indexes contain, a limitation returned to in the final section. Every reference retained was checked against Crossref metadata for author list, title, year, journal, volume, issue, pagination or article number, and digital object identifier resolution, and any record whose metadata could not be confirmed in full was discarded rather than reported with partial detail.

2.3 Search Strategy and Search Period

Search concepts were derived from the review question and combined with Boolean operators. The first concept covered the editing technology, using terms including CRISPR, Cas9, Cas12a, genome editing, gene editing, base editing and prime editing. The second covered the target crops, using vegetable, tomato, *Solanum lycopersicum*, pepper, *Capsicum*, potato, *Solanum tuberosum*, lettuce, *Lactuca sativa*, cucumber, melon, watermelon, *Cucurbita*, *Brassica*, cabbage, cauliflower and broccoli. The third covered climate-relevant stress and outcome terms, including heat tolerance, thermotolerance, drought tolerance, water deficit, salinity, salt stress, chilling tolerance, climate resilience, yield stability, pollen viability and stomatal conductance. A fourth concept captured implementation and translation, using regeneration, transformation efficiency, recalcitrance, field trial, off-target, regulation, regulatory, intellectual property and public acceptance.

Representative strings executed in Europe PMC included (TITLE:(CRISPR OR "genome editing") AND TITLE:(vegetable*)), (TITLE:(CRISPR) AND TITLE:(tomato) AND TITLE:(thermotolerance OR "heat stress" OR "heat tolerance")), (TITLE:(CRISPR) AND TITLE:(salt OR salinity) AND (tomato OR Solanum)), (TITLE:("prime editing") AND (tomato OR Solanum)), and (TITLE:(CRISPR OR "genome editing") AND TITLE:(transformation OR regeneration) AND (recalcitrant OR genotype)). Crossref Metadata Search was queried with bibliographic strings targeting specific studies identified through citation tracing. Searches were date-limited using first-publication-date filters.

The search period ran from 1 January 2015 to 10 June 2026. The starting year reflects the point at which heritable Cas9-induced mutations were first reported in horticultural Brassicaceae (Lawrenson et al., 2015), so that earlier years contain no eligible primary evidence on edited vegetable crops. Foundational publications preceding this date were retained where they were necessary to explain conceptual development or established methodology, and methodological references concerning review conduct were not date-restricted. The final search date was 10 June 2026.

2.4 Eligibility Criteria

Eligible publications were peer-reviewed journal articles reporting original research or substantive review of genome editing in the defined vegetable groups, of climate-related stress physiology in those groups, or of the regulatory, economic and social conditions bearing on deployment of edited crops. Methodological articles on narrative review conduct were eligible irrespective of subject area. Studies of cereals, legume grain crops, oilseeds, fruit trees, ornamentals and model species were eligible only where they supplied methodological evidence, such as genome-wide off-target assessment or delivery innovation, that has no vegetable-crop equivalent and that bears directly on the appraisal.

Publications were excluded when they were preprints for which peer-reviewed equivalents existed, conference abstracts, book chapters lacking independent peer review, commentary or news items, promotional material, or records whose bibliographic details could not be verified in full. Editorials and corrigenda were not treated as primary evidence. Language was restricted to English. Retracted articles were excluded, and no retracted source is cited. Where an article had an associated correction notice, the corrected version was used and the underlying finding was treated with additional caution.

2.5 Screening, Duplicate Handling and Study Selection

Records returned by each search were screened first on title and abstract for topical relevance to the review objectives, then assessed at full text where the abstract indicated that the study reported an edited allele, a climate-relevant phenotype, a delivery or regeneration method applicable to vegetables, or governance evidence. Duplicates arising from overlapping index coverage, from preprint and version-of-record pairs, and from indexing of the same article under variant titles were identified by digital object identifier and by title and author matching, and only the version of record was retained. Where a preprint and a published article described the same work, the published article was used.

Selection was purposive rather than exhaustive. Studies were retained on the basis of relevance to a defined theme, adequacy of reported methods, contribution of evidence not available elsewhere, and capacity to test rather than merely illustrate an interpretation, with deliberate retention of studies reporting negative or unfavourable results. Citation count was not used as an inclusion criterion. Sources that could not be accessed in full text, or whose methods were reported too sparsely to permit appraisal, were not cited. No formal screening counts are reported, because the selection process was iterative and interpretive rather than protocol-driven, and reporting counts would imply a systematic procedure that was not performed. No flow diagram is presented for the same reason.

2.6 Critical Appraisal and Evidence Synthesis

Each primary study was appraised against criteria appropriate to plant molecular breeding rather than against a clinical instrument, and no formal risk-of-bias score was assigned because no validated tool exists for this literature and the reporting in many studies is too sparse to support one. The criteria applied were the appropriateness of the stress protocol to the trait claimed, the developmental stage assessed, the growth environment and whether it approximated production conditions, the number of independent edited lines and generations analysed, the nature of the control genotype and whether transgene-free segregants or azygous siblings were used, the relationship between the measured endpoint and agronomic performance, the treatment of off-target and tissue-culture-derived variation, and the consistency of the finding with independent evidence.

Themes were developed inductively from the retained corpus rather than imposed in advance. Initial coding by crop and target gene was abandoned because it reproduced the catalogue structure of existing reviews; the final organisation follows the inferential problems that recur across crops, namely allelic resolution and delivery, stress-specific evidence quality, directional inconsistency, evaluation environment, biotic interaction and deployment conditions. Where studies disagreed, the disagreement was retained and interpreted through differences in stress protocol, developmental stage, genetic background and endpoint, rather than resolved by preferring the more recent or more highly cited result. Confidence statements attached to each conclusion reflect the number of independent studies, the diversity of conditions under which the result was reproduced, and the proximity of the endpoint to agronomic performance.

3. The Precision-Breeding Toolkit and Its Limits in Vegetable Species

3.1 Editing Modalities and the Range of Accessible Allelic Variation

The functional reach of an editing platform is set by the class of sequence change it can install, and the vegetable literature is dominated by the narrowest of these. Cas9-induced double-strand breaks repaired by non-homologous end joining produce small insertions and deletions that, in coding sequence, generally yield null or strongly hypomorphic alleles. This suffices for reverse genetics and for traits whose improvement genuinely requires gene inactivation, but it restricts the accessible phenotypic space to whatever loss of function delivers. Many climate-resilience traits are quantitative and dosage sensitive, and complete inactivation of a stress-signalling component is as likely to be deleterious as beneficial.

Regulatory-sequence editing widened this space substantially. Mutagenesis of the *CLAVATA3* promoter in tomato generated an allelic series spanning a continuum of locule number and fruit size, showing that transcriptional output could be tuned rather than switched off and that novel quantitative variation could be created within a fixed genetic background (Rodríguez-Leal et al., 2017). Dissection of the *cis*-regulatory region of an ancient homeobox gene across Solanaceous species subsequently demonstrated that promoter alleles separate pleiotropic functions that null alleles conflate, so that regulatory editing is not merely a weaker version of knockout but a qualitatively different intervention (Hendelman et al., 2021). Analysis of structural variation across tomato genomes reinforced the point from the natural-variation side, showing that a large fraction of agronomically consequential variation is regulatory and structural rather than coding (Alonge et al., 2020). Promoter and enhancer replacement is now being formalised as a breeding strategy in its own right (Nobusawa et al., 2026), although the demonstrated applications in vegetables remain few relative to cereals.

Base editing installs transition substitutions without a double-strand break and has been established in tomato and potato using Agrobacterium-delivered cytidine base editors, with edited plants recoverable free of the editing construct (Veillet et al., 2019). Delivery of *in vitro* transcribed base editors to lettuce protoplasts extended the approach to a leafy vegetable without introducing DNA (Lee et al., 2025). The most instructive application to date used base editing to repair a deleterious variant fixed during tomato domestication in a floral regulator, restoring ancestral function rather than removing it (Glaus et al., 2025). That study illustrates a mode of action unavailable to knockout approaches, namely the correction of accumulated deleterious variation, which is conceptually well suited to resilience traits eroded by domestication bottlenecks.

Prime editing extends the accessible range further, permitting arbitrary short substitutions, insertions and deletions. Efficiency in dicotyledonous species was long the constraint, and optimisation of prime editor architecture and pegRNA design was required before heritable, intended edits were obtained routinely in tomato (Vu et al., 2024). The most consequential application in the vegetable literature used high-efficiency prime editing to insert a ten-base-pair heat-shock element into the promoters of cell-wall invertase genes in elite tomato and rice cultivars, conferring heat-responsive upregulation of carbon partitioning to fruit and grain; per-plot yield under heat stress increased by 33 per cent in the tomato cultivar Ailsa Craig relative to heat-stressed controls, with the effect reproduced in field as well as controlled environments and without reported quality penalties (Lou et al., 2025). This result matters less for the specific target than for what it demonstrates about design: a defined regulatory insertion, an elite background, a yield endpoint and a field environment together produce inference of a different order from that supported by the knockout literature.

3.2 Delivery and Regeneration as the Binding Constraint

Nuclease performance is rarely the factor limiting progress in vegetable crops. The limiting factor is the ability to deliver editing reagents into cells that will regenerate into fertile plants, and this ability is strongly genotype dependent. Heritable Cas9-induced mutations were obtained in *Brassica oleracea* L. at an early stage, but the efficiency reported was low relative to that achieved in model species, and the transformation and regeneration protocol rather than the nuclease determined throughput (Lawrenson et al., 2015). Comparable constraints operate across cole crops, cucurbits and *Capsicum*, and reviews of *Brassica* stress-tolerance editing

identify regeneration capacity as the principal practical obstacle to translating validated targets into edited lines (Ton et al., 2025). The practical consequence is that most published edits in vegetables exist in a small set of transformation-competent genotypes, typically Micro-Tom or Ailsa Craig in tomato, rather than in cultivars grown commercially.

Table 1. Editing modalities applied to vegetable crops, the allelic variation each can generate, and the principal constraint on each

Modality	Molecular outcome	Allelic range accessible	Demonstrated application in vegetable species	Supporting references
Cas9 nuclease editing of coding sequence	Double-strand break repaired by non-homologous end joining; small indels	Null and strong hypomorphic alleles only; direction of effect fixed by gene function	Extensive across tomato, potato, lettuce, cucumber and *Brassica oleracea*; the majority of published stress-related edits	Chandrasekaran et al. (2016); Lawrenson et al. (2015); Wang et al. (2017)
Cas9 editing of promoter and cis-regulatory sequence	Deletions and rearrangements within regulatory regions	Continuous series of expression-level alleles; separation of pleiotropic functions	Established in tomato for architecture and fruit traits; limited application to stress traits	Hendelman et al. (2021); Nobusawa et al. (2026); Rodríguez-Leal et al. (2017)
Cytosine and adenine base editing	Transition substitutions without double-strand break	Defined amino-acid substitutions; repair of deleterious variants	Demonstrated in tomato, potato and lettuce; one application to a domestication variant	Glaus et al. (2025); Lee et al. (2025); Veillet et al. (2019)
Prime editing	Reverse-transcriptase-templated substitutions, short insertions and deletions	Arbitrary short sequence changes, including insertion of regulatory motifs	Heritable edits in tomato; one field-evaluated application to heat-responsive expression	Lou et al. (2025); Vu et al. (2024)
DNA-free ribonucleoprotein delivery	Transient nuclease activity without integrated sequence	Same range as the nuclease delivered; constrained by regeneration	Protoplast-derived edited plants in tomato and lettuce; *in planta* delivery in melon	Choi et al. (2022); Liu et al. (2022); Sasaki et al. (2025)
Tissue-culture-independent delivery	Viral or nanoparticle delivery of compact nucleases	Determined by cargo capacity of the delivery vehicle	Demonstrated in model and tree species; not yet reported for a climate trait in a commercial vegetable cultivar	Gupta et al. (2025); Hu et al. (2026)

Note. Indel, insertion or deletion. Entries describe the state of demonstrated application within the vegetable groups defined in Section 1.1 and are not exhaustive of all reported uses of each modality across plants

Two lines of work address this constraint directly. Expression of morphogenic regulators improves regeneration efficiency across species; a chimeric fusion of GROWTH-REGULATING FACTOR 4 and its interacting factor increased transformation efficiency substantially in several crops and reduced dependence on genotype (Debernardi et al., 2020). Induction of *de novo* meristems on cut seedling tissue provides an alternative route that avoids conventional tissue culture altogether, producing edited shoots directly (Maher et al., 2020). Both approaches were demonstrated principally outside the vegetable groups considered here, and the extent to which they transfer to cucurbits and Brassicaceae remains an open question rather than a settled result.

A second strategy removes DNA from the process. Regeneration of cultivated tomato from protoplasts transfected with ribonucleoprotein complexes has been established, yielding edited plants without integrated sequence (Liu et al., 2022), and the same principle produced late-bolting lettuce from mesophyll protoplasts (Choi et al., 2022) and long-shelf-life melon by *in planta* ribonucleoprotein delivery (Sasaki et al., 2025). Protoplast regeneration is itself genotype dependent and labour intensive, so the approach substitutes one bottleneck for another rather than eliminating it. Viral delivery of compact nucleases offers a tissue-culture-independent route and has produced heritable, transgene-free edits using a miniature Cas12f system (Hu et al., 2026), while nanoparticle-mediated delivery is advancing conceptually (Gupta et al., 2025). Both remain mechanistically plausible rather than demonstrated at breeding scale in vegetable crops, and neither has yet been reported to deliver a climate-resilience allele into a commercial vegetable cultivar.

Table 1 compares the editing modalities against the allelic range each can access, the extent of demonstrated application in vegetable species, and the principal constraint on each. The comparison makes clear that the modalities capable of the finest allelic control are those with the least demonstrated deployment in vegetables, and that the dominance of knockout approaches in the published record reflects accessibility rather than suitability to the traits at issue. It also shows that constraints differ in kind: for knockout editing the limitation is conceptual, in that loss of function may not be the change required, whereas for prime and base editing the limitation is operational, in that the necessary delivery and regeneration systems exist for few genotypes.

4. Engineering Abiotic-Stress Resilience: What the Evidence Supports

The abiotic-stress editing literature in vegetables is organised below by stress rather than by species, because the recurring inferential problems are stress specific. Across all four stresses the same structural feature appears: the experiments are designed to test gene function and are reported in language that implies agronomic improvement.

4.1 Thermotolerance and Reproductive Stability

Reproductive development is the stage at which heat converts into yield loss in fruit vegetables, through pollen abortion, impaired anther dehiscence and failure of fertilisation, so evidence bearing on pollen performance carries particular weight. Work on tomato pollen thermotolerance has established mechanistic detail without necessarily involving editing. Overexpression of the heat-shock transcription factor HsfA1a improved pollen thermotolerance through enhanced antioxidant capacity and protein repair and degradation, identifying a signalling node with plausible utility (Xie et al., 2022). Genetic and chemical dissection of flavonol biosynthesis showed that flavonols maintain ROS homeostasis during pollen germination and tube elongation and that flavonol-deficient mutants lose thermotolerance, while restoration of flavonols rescues it (Postiglione et al., 2024). These studies support the proposition that ROS management in pollen is a tractable target. Neither establishes that an edited allele in a commercial genotype improves fruit set under field heat.

Reproductive avoidance offers a different route. Loss of function of the MADS-box gene *SlAGAMOUS-LIKE 6* produces facultative parthenocarpy in tomato, allowing fruit development in the absence of successful fertilisation while leaving other floral and vegetative traits largely unaffected (Klap et al., 2017). Because heat-induced yield loss operates substantially through fertilisation failure, decoupling fruit set from fertilisation addresses the mechanism rather than the symptom. The evidence supports the phenotype robustly under the conditions tested; it does not extend to multi-season field demonstration of yield protection under heat, and parthenocarpy carries consequences for seed production and for fruit quality attributes that require assessment before deployment.

Direct editing for thermotolerance has produced one result of unusual quality and a small number of reverse-genetic findings. Knockout of *SlMAPK3* by Cas9 produced tomato mutants that showed less wilting and membrane damage under heat, lower ROS accumulation, higher antioxidant enzyme activity and elevated expression of heat-shock factor and heat-shock protein genes, supporting the conclusion that *SlMAPK3* acts as a negative regulator of thermotolerance (Yu et al., 2019). The conclusion about gene function is well supported by the data presented. The step from that conclusion to a heat-tolerant cultivar is not taken in the study and has not been taken since: the assessment used seedlings under controlled heat treatment, and no fruit-yield endpoint was measured.

Against this background, the prime-editing insertion of a heat-shock element into cell-wall invertase promoters stands apart (Lou et al., 2025). The intervention was designed from a physiological hypothesis about source-sink limitation under heat rather than selected from a list of stress-responsive genes; the edit was a defined regulatory insertion rather than a knockout; the background was an elite cultivar; and the endpoint was per-plot yield measured under both controlled and field conditions. The reported yield advantage under heat stress in tomato was accompanied by a comparable effect in rice, which provides a form of independent replication across a distant species and reduces the probability that the result reflects a background-specific artefact. Confidence in this finding is correspondingly higher than in any other thermotolerance result in the vegetable editing literature, although it remains a single study and its durability across seasons, sites and cultivars is untested.

Leafy vegetables face a different heat problem, namely premature reproductive transition and impaired germination. Editing that delays bolting in lettuce was achieved through protoplast-based, DNA-free mutagenesis, producing late-bolting plants (Choi et al., 2022). High-resolution analysis of Cas9-induced modification of *NCED4* in lettuce, a gene controlling thermoinhibition of germination, characterised editing efficiency, heritability and the spectrum of editing outcomes in detail (Bertier et al., 2018); the study is methodologically strong on editing performance and comparatively modest on demonstrated field benefit. Knockout of *SPL13* was reported to increase lettuce yield substantially (Beracochea et al., 2023), a result reported as a brief communication with limited experimental detail, so the effect size should be treated as provisional until independently reproduced.

Set against the editing literature, quantitative-genetic analyses of tomato heat response resolve numerous loci of small effect whose expression varies with environment (Bineau et al., 2021; Wen et al., 2019). The contrast is informative rather than merely descriptive: it indicates that thermotolerance in the standing germplasm is highly polygenic, which weakens the prior expectation that editing one or two loci will produce a large and stable field advantage, and correspondingly strengthens the case for interventions that alter a physiological bottleneck directly, as regulatory engineering of carbon partitioning does.

4.2 Water Deficit

The drought literature illustrates the interpretive problem in its clearest form, because several of the best-known studies report that editing reduced tolerance. Cas9-mediated knockout of *SlMAPK3* produced tomato mutants with more severe wilting, higher hydrogen peroxide content, lower antioxidant enzyme activity and greater membrane damage under drought than the wild type, together with altered expression of drought-responsive genes (Wang et al., 2017). Knockout of *SlNPR1* likewise reduced drought tolerance, with mutants showing greater stomatal aperture, lower antioxidant enzyme activity and increased hydrogen peroxide and malondialdehyde accumulation (R. Li et al., 2019). Both studies are competent reverse genetics establishing that the targeted genes contribute positively to drought responses. Neither produces a drought-tolerant plant, and citing them as instances of CRISPR-based drought improvement, as catalogue reviews sometimes do, inverts their finding.

Editing that improved water-related performance has come from targeting negative regulators and from altering stomatal behaviour. Loss of function of *SlARF4* altered stomatal function, reduced stomatal conductance, increased leaf relative water content and abscisic acid concentration, and improved tolerance of osmotic and salt stress, with the Cas9 mutant reproducing the phenotype obtained by antisense downregulation (Bouzroud et al., 2020). The convergence of two independent perturbation methods on the same phenotype strengthens the causal inference considerably. The endpoints remain physiological rather than agronomic, and

reduced stomatal conductance carries an expected cost in carbon assimilation that the study does not quantify under well-watered conditions.

The most agronomically framed drought study in the corpus targeted *StCBP80*, a cap-binding protein acting in abscisic acid signalling, in the tetraploid commercial potato cultivar Spunta. Because complete inactivation of all four alleles is difficult in a tetraploid, the lines characterised carried edits at two or three alleles; under restricted water they showed reduced transpiration, improved leaf area index, altered expression of drought-responsive genes and smaller yield penalties in both biomass and tuber production than unedited controls (Decima Oneto et al., 2025). The inclusion of a tuber-yield endpoint and the use of a commercial rather than a model background make this study more informative than most of the tomato work. Its limitations are that the water-deficit treatment was imposed under controlled conditions, that partial allelic editing complicates interpretation of dosage, and that the article carries a subsequent correction notice, so independent confirmation in additional backgrounds and under field water deficit remains necessary.

Table 2. Representative genome-editing studies of climate-relevant abiotic stress in vegetable crops, classified by edit type, endpoint and evaluation environment

Crop and target	Edit type	Reported phenotype	Endpoint measured	Evaluation environment and stage	Supporting references
Tomato *SlMAPK3*	Knockout	Improved heat tolerance; *SlMAPK3* acts as a negative regulator	Wilting, ROS content, antioxidant enzyme activity, HSF and HSP transcripts	Controlled heat treatment; seedling stage	Yu et al. (2019)
Tomato *SlMAPK3*	Knockout	Reduced drought tolerance	Wilting, hydrogen peroxide, antioxidant enzymes, membrane damage	Controlled water withholding; vegetative stage	Wang et al. (2017)
Tomato *SlNPR1*	Knockout	Reduced drought tolerance	Stomatal aperture, antioxidant enzymes, hydrogen peroxide, malondialdehyde	Controlled water withholding; vegetative stage	R. Li et al. (2019)
Tomato *SlCBF1*	Knockout	Reduced chilling tolerance	Electrolyte leakage, malondialdehyde, hydrogen peroxide, proline and protein content, phytohormones	Controlled chilling; vegetative stage	R. Li et al. (2018)
Tomato *SlARF4*	Knockout, with antisense confirmation	Improved salinity and osmotic tolerance via stomatal and abscisic acid changes	Stomatal conductance, relative water content, abscisic acid, chlorophyll	Controlled salt and osmotic treatment; vegetative stage	Bouzroud et al. (2020)
Tomato *SlHyPRP1*	Multiplexed domain excision	Improved salinity tolerance	Germination and growth under salinity	Controlled salinity; germination and vegetative stages	Tran et al. (2021)
Tomato *SlAGL6*	Knockout	Facultative parthenocarpy, decoupling fruit set from fertilisation	Fruit set and fruit characteristics	Controlled conditions; reproductive stage	Klap et al. (2017)
Tomato cell-wall invertase promoters	Prime-editing insertion of a heat-shock element	Heat-responsive upregulation of carbon partitioning; higher yield under heat	Per-plot fruit yield under heat stress	Controlled and field environments; to harvest	Lou et al. (2025)
Potato *StCBP80* in cultivar Spunta	Partial knockout of two or three alleles in a tetraploid	Reduced transpiration and smaller yield penalty under water deficit	Transpiration, leaf area index, biomass and tuber yield	Controlled water restriction; to tuber harvest	Decima Oneto et al. (2025)
Lettuce *NCED4*	Knockout	Modification of a regulator of germination thermoinhibition	Editing efficiency, heritability and mutation spectrum	Controlled conditions; germination	Bertier et al. (2018)
Lettuce bolting-related locus	Knockout via DNA-free protoplast editing	Delayed bolting	Bolting time	Controlled conditions; vegetative to reproductive transition	Choi et al. (2022)

Note. HSF, heat-shock transcription factor; HSP, heat-shock protein; ROS, reactive oxygen species. Entries are representative of the identified literature rather than an exhaustive listing, and reported phenotypes are stated as claimed by the source study

A structural weakness runs through this subsection. Drought is imposed in most studies by withholding water from potted plants for a fixed period, a protocol that produces rapid, severe and largely uniform stress unlike the progressive, heterogeneous water deficit

experienced in the field. Endpoints are dominated by wilting scores, electrolyte leakage, malondialdehyde and hydrogen peroxide concentrations, and antioxidant enzyme activities. These variables index cellular damage rather than productivity, and their relationship to marketable yield under field drought has not been established for any of the tomato loci discussed. The potato work is the partial exception, in that it measured tuber yield, but the water-deficit treatment remained a controlled one. Confidence that any published edited allele confers field-relevant drought resilience in a vegetable crop is therefore low, and the gap is one of experimental design rather than of editing capability.

4.3 Salinity

Salinity editing in vegetables is dominated by a small number of tomato studies. Multiplexed Cas9 editing was used to excise specific functional domains of the hybrid proline-rich protein *SlHyPRP1*, a negative regulator of salt responses, rather than to inactivate the gene entirely; precise removal of the negative-response domains produced lines tolerant of high salinity at the germination and vegetative stages (Tran et al., 2021). The design is notable because it demonstrates domain-level engineering of a multidomain protein using standard Cas9 reagents, which recovers some of the allelic precision otherwise requiring base or prime editing. The limitation is equally clear and is acknowledged by the authors: tolerance was assessed at germination and during vegetative growth under defined experimental conditions, and salt effects on fruit yield and quality, which are what determine commercial viability under saline irrigation, were not measured.

The *SlARF4* work described above also reported improved tolerance of salinity alongside osmotic stress, mediated through stomatal and abscisic acid changes (Bouzroud et al., 2020). Because osmotic and ionic components of salt stress act on different timescales and through different mechanisms, evidence drawn from short-term assays conflates them, and the durability of tolerance under prolonged sodium accumulation is not addressed. Across the salinity literature, no study in a vegetable crop reports edited alleles evaluated to harvest under saline field or greenhouse irrigation with yield endpoints. This is the largest single evidential gap identified in this review, because salinisation of irrigated vegetable production is a comparatively predictable consequence of climate-driven water scarcity and because the trait has clearer physiological targets than drought.

4.4 Chilling and Low-Temperature Exposure

Chilling receives less attention than heat, which is understandable given the direction of climate change but is not fully justified, since increased variability includes late frosts and cold snaps against a background of earlier planting. The principal editing study knocked out *SlCBF1* in tomato and found that mutants suffered more severe chilling injury, with higher electrolyte leakage, malondialdehyde and hydrogen peroxide concentrations, lower proline and protein contents, altered phytohormone profiles and downregulation of C-repeat binding factor pathway genes (R. Li et al., 2018). As with the drought studies from the same research programme, the result confirms that the targeted gene contributes positively to tolerance and therefore identifies a locus whose enhancement, not inactivation, might be beneficial. No study in a vegetable crop has yet used base or prime editing to increase C-repeat binding factor pathway output rather than remove it, which is the intervention the finding implies.

Table 2 summarises representative studies across the four stresses, recording for each the nature of the edit, the reported phenotype, the evaluation environment and the developmental stage assessed. Reading the table by column rather than by row exposes the pattern that motivates this review: the great majority of entries describe knockouts in model genotypes assessed under controlled conditions using damage proxies, and the single entry reporting a field-measured yield endpoint is also the single entry describing a designed regulatory insertion in an elite background. The table also shows that the direction of the reported effect is unfavourable in three of the entries, which is a feature of the evidence base rather than a selection artefact of this review.

5. Directional Inconsistency, Pleiotropy and Trade-offs

5.1 The Same Locus, Opposite Conclusions

The clearest test of whether the vegetable editing literature is internally coherent is provided by *SlMAPK3*, for which two studies from the same research programme, using comparable editing reagents and overlapping analytical panels, reached opposite conclusions about the consequence of knockout. Loss of function reduced drought tolerance (Wang et al., 2017) and improved heat tolerance (Yu et al., 2019). Neither result is obviously flawed, and the two studies do not contradict one another in the strict sense, because different stresses were applied. Taken together, though, they undermine any claim that a gene can be classified as a stress-tolerance gene without qualification by stress type.

A plausible mechanistic reconciliation is available. Both studies converge on ROS homeostasis as the mediating process, and ROS operate simultaneously as damaging agents and as signalling molecules, with the optimum concentration differing between stresses and tissues. If *SlMAPK3* sustains ROS-dependent signalling that is protective under progressive water deficit but that pushes accumulation beyond the damage threshold during acute heat, then removing the kinase would be expected to have opposite consequences under the two regimes. This interpretation is consistent with both datasets but has not been tested directly, for instance by imposing combined heat and drought on the same mutant lines, which is the treatment most relevant to field conditions and which neither study performed.

The pattern extends beyond a single locus. Knockout of *SlNPR1* reduced drought tolerance (R. Li et al., 2019) and knockout of *SlCBF1* reduced chilling tolerance (R. Li et al., 2018), so that three of the most frequently cited tomato stress-editing studies report that editing made plants less tolerant. A literature in which unfavourable results are this prominent is unlikely to be strongly affected

by publication bias against negative findings, which is a genuine strength. The corresponding weakness is that the applied narrative built around these studies is not supported by them, and reviews that list these loci among CRISPR contributions to stress tolerance without recording the direction of effect propagate an error that is easy to avoid.

5.2 Pleiotropy, Trade-Offs and the Cost of Resilience

Resilience alleles are expected to carry costs, because stress-response pathways interact with growth and reproduction. Evidence on this point in edited vegetables is thin but not absent. The promoter allelic series at *CLAVATA3* demonstrated that intermediate expression alleles can occupy phenotypic positions unavailable to null alleles, which is the mechanism by which trade-offs may be tuned rather than merely accepted (Rodríguez-Leal et al., 2017). Regulatory dissection of a conserved homeobox gene showed that promoter alleles can separate developmental functions that null alleles combine, establishing that pleiotropy is often a property of the perturbation rather than an irreducible property of the gene (Hendelman et al., 2021).

Direct measurement of costs is rarer. Editing of a susceptibility gene in potato improved *Phytophthora* resistance without a detectable growth penalty (Bi et al., 2024), and editing of *StDMR6-1* produced plants less affected by several stress conditions rather than trading one tolerance for another (Karlsson et al., 2024). These results show that penalty assessment is feasible and that penalties are not universal. They also highlight how seldom such assessment is performed: the abiotic-stress studies summarised in Table 2 report, almost without exception, only the stressed comparison, so that any growth or yield cost under non-stress conditions would go undetected. Where a physiological mechanism implies a cost, as reduced stomatal conductance implies reduced assimilation (Bouzroud et al., 2020), the absence of measurement is a substantive omission rather than a reporting formality.

Parthenocarpy illustrates the same issue in a reproductive context. Decoupling fruit set from fertilisation is advantageous under heat but alters seed production, which matters for cultivar maintenance and for growers who save seed, and may affect fruit composition (Klap et al., 2017). Whether the net effect is favourable depends on the production system, and the published evidence does not permit that judgement to be made.

Table 3 sets out the principal inconsistencies and unresolved tensions identified across the corpus together with the explanations that the available evidence supports and a statement of the confidence attaching to each. The table is analytical rather than summary: the explanations proposed are hypotheses generated by this synthesis, and the confidence column records how far each is currently testable rather than tested. Its main implication is that most apparent contradictions in this literature dissolve once stress type, developmental stage and endpoint are specified, which in turn means that the contradictions are largely artefacts of reporting practice and could be removed by better specification of claims.

Table 3. Directionally inconsistent or unresolved findings in the vegetable editing literature, with plausible explanations and current confidence

Observation	Contrasting or complicating evidence	Plausible explanation supported by available data	Confidence in the explanation	Supporting references
Knockout of *SlMAPK3* improves heat tolerance	Knockout of the same gene reduces drought tolerance	Stress-specific optima for reactive oxygen species signalling; the kinase is protective under progressive water deficit and damaging under acute heat	Low to moderate; consistent with both datasets but not directly tested	Wang et al. (2017); Yu et al. (2019)
Editing is presented as a route to stress tolerance	Three prominent tomato studies report reduced tolerance after editing	Reverse-genetic designs establish gene function; applied framing is applied post hoc in reviews rather than supported by the primary data	Moderate to high; evident from the study designs themselves	R. Li et al. (2018); R. Li et al. (2019); Wang et al. (2017)
Single-gene edits are expected to deliver field heat tolerance	Quantitative genetic analyses resolve many loci of small effect with strong environmental interaction	Standing thermotolerance variation is highly polygenic; large single-locus gains are more likely from altering a physiological bottleneck than from editing a stress-responsive regulator	Moderate; supported by convergent QTL evidence and by the one field-validated editing result	Bineau et al. (2021); Lou et al. (2025); Wen et al. (2019)
Loss-of-function alleles are assumed to carry growth penalties	Susceptibility-gene edits in potato show resistance gains without detectable growth cost	Penalties depend on the gene and the pathway; they are testable and should not be assumed in either direction	Moderate; based on few studies that measured cost explicitly	Bi et al. (2024); Karlsson et al. (2024)
Improved tolerance is inferred from cellular damage proxies	Yield endpoints appear in only a small minority of studies, and no vegetable study reports edited alleles evaluated to harvest under field salinity	The proxy-to-yield relationship is untested for most loci, so tolerance claims rest on an unvalidated inferential step	High; the absence of such endpoints is verifiable from the primary reports	Bouzroud et al. (2020); Decima Oneto et al. (2025); Tran et al. (2021)

Note. QTL, quantitative trait locus. Explanations are interpretations developed in the present synthesis and are stated as hypotheses; the confidence column refers to the explanation, not to the underlying observations

6. Methodological Quality and the Translation Gap

6.1 Evaluation Environment, Developmental Stage and Endpoint

Three design choices determine how far a stress-editing result can be extrapolated, and the vegetable literature makes the same choices repeatedly. The first is the evaluation environment. Almost all abiotic-stress editing in vegetables has been assessed in growth chambers, glasshouses or pot experiments, where stress is imposed abruptly and uniformly. Field environments differ in the rate at which stress develops, in the spatial heterogeneity of soil water and salinity, in the coincidence of multiple stresses, and in the presence of pathogens and competitors. Field evaluation is not a formality appended to laboratory work; it frequently reverses conclusions, because alleles that protect against acute stress may confer no advantage or a disadvantage under gradual stress accompanied by compensatory acclimation. Two studies in the corpus escape this limitation. The prime-editing intervention in carbon partitioning was evaluated in field as well as controlled environments and reported yield gains in both (Lou et al., 2025), and susceptibility-gene mutants in potato were assessed in four consecutive years of field trials at a site with a complex pathogen population (Karlsson et al., 2024). Both, notably, report favourable outcomes without the trade-offs that field testing is often expected to expose, which suggests that field evaluation is avoided for reasons of cost and regulatory friction rather than because it is expected to be unflattering.

The second choice is developmental stage. Salinity tolerance assessed at germination and early vegetative growth (Tran et al., 2021) addresses a real constraint on stand establishment but says little about ion accumulation over a full season, and heat tolerance assessed in seedlings (Yu et al., 2019) does not address the reproductive stage at which heat causes most yield loss. Where a trait has a well-defined critical window, evidence obtained outside that window carries limited weight regardless of its internal quality.

The third choice is the endpoint. Electrolyte leakage, malondialdehyde concentration, hydrogen peroxide concentration, antioxidant enzyme activity and wilting score dominate the corpus. These are informative about cellular damage and about the mechanism through which a gene acts, and they are inexpensive and rapid. They are not measures of agricultural performance, and no study in this literature has established a quantitative relationship between them and marketable yield under stress for any vegetable species. When a study reports lower malondialdehyde in an edited line and the accompanying discussion describes the line as stress tolerant, an inferential step has been taken that the data do not support. The studies that measured yield directly (Decima Oneto et al., 2025; Karlsson et al., 2024; Lou et al., 2025) show that yield endpoints are attainable, which makes their rarity a matter of convention rather than necessity.

6.2 Genetic Background, Controls and Unintended Variation

Most published edits in vegetables exist in genotypes chosen for transformation competence. Micro-Tom and Ailsa Craig dominate the tomato literature; both are experimentally convenient and neither is grown commercially at scale. Because the effect of an allele depends on the genetic background in which it acts, and because stress-response networks are precisely the kind of network in which epistasis is expected, results obtained in these backgrounds establish that an allele can produce a phenotype rather than that it will produce it in cultivars of interest. The prime-editing and potato studies that used elite or commercial backgrounds (Decima Oneto et al., 2025; Lou et al., 2025) are the exceptions that reveal the norm.

Control design is a second recurring weakness. Comparison of edited lines with the untransformed wild type conflates the effect of the edit with the effects of tissue culture and transformation, both of which generate heritable somaclonal variation. Comparison with azygous or transgene-free segregating siblings removes this confound, and reporting is often insufficient to determine which comparison was made. The number of independent edited lines analysed is frequently two, which is adequate to show that a phenotype recurs across independent transformation events but provides little protection against a shared culture-derived artefact.

Off-target editing receives disproportionate attention relative to its likely contribution. Whole-genome sequencing of large numbers of Cas9-edited and Cas12a-edited rice lines found that off-target mutations were rare and that the great majority of sequence differences from the parental line arose from tissue culture and from natural variation rather than from the nuclease (Tang et al., 2018). A broad appraisal of off-target change in plant genome editing reached compatible conclusions and set the phenomenon against the mutational load generated by conventional and mutagenesis breeding (Graham et al., 2020). The evidence from rice is not automatically transferable to polyploid vegetables with larger repetitive fractions, and comparable whole-genome analyses in vegetable crops are scarce, so the appropriate position is that off-target effects are probably a minor confounder relative to culture-derived variation but that this has not been demonstrated directly in most vegetable species. The practical implication is that resources currently directed at exhaustive off-target screening would be better spent on backcrossing, on azygous controls and on multi-line replication.

Table 4 records the methodological limitations that recur across the corpus, the way each manifests, the consequence for inference and a feasible mitigation. The mitigations listed are deliberately conventional, since none requires methodological innovation; the limitations persist because of the incentives operating on publication rather than because they are technically difficult to address. The table is intended to be used as an appraisal checklist when reading individual studies, and its principal implication is that the largest gains in evidential quality would come from changes in evaluation design rather than from further improvement in editing reagents.

Table 4. Recurring methodological limitations across the vegetable genome-editing literature and feasible mitigations

Limitation	How it manifests in the corpus	Consequence for inference	Feasible mitigation	Supporting references
Controlled evaluation environments	Growth chambers, glasshouses and pot experiments with abrupt, uniform stress	Extrapolation to field conditions is unwarranted; acclimation and stress heterogeneity are absent	Multi-site, multi-season field evaluation with managed stress gradients	Karlsson et al. (2024); Lou et al. (2025)
Damage proxies used as tolerance measures	Electrolyte leakage, malondialdehyde, hydrogen peroxide and antioxidant enzyme activity dominate reported endpoints	The proxy-to-yield relationship is unvalidated, so tolerance claims exceed the data	Report marketable yield and quality alongside physiological variables	Decima Oneto et al. (2025); R. Li et al. (2019); Wang et al. (2017)
Non-commercial genetic backgrounds	Micro-Tom and Ailsa Craig dominate the tomato literature	Background-dependent effects and epistasis are unassessed; transferability is unknown	Edit elite backgrounds directly or introgress and re-evaluate across cultivars	Decima Oneto et al. (2025); Lou et al. (2025)
Developmental stage mismatch	Seedling or germination assays used for traits whose critical window is reproductive	Evidence falls outside the window in which the trait determines yield	Assess at the stage at which the stress causes yield loss	Tran et al. (2021); Yu et al. (2019)
Control design and line number	Comparison with untransformed wild type; typically two independent lines	Tissue-culture-derived variation is confounded with the edit	Use azygous or transgene-free segregant controls and additional independent lines	Graham et al. (2020); Tang et al. (2018)
Single-stress protocols	Stresses imposed individually rather than in the combinations that occur in the field	Interactions between stresses, which can reverse the sign of an effect, are not detected	Impose combined heat and water deficit on the same lines	Wang et al. (2017); Yu et al. (2019)
Absence of cost measurement	Only the stressed comparison is reported in most studies	Growth or yield penalties under non-stress conditions would go undetected	Include well-watered and non-stressed controls with yield endpoints	Bi et al. (2024); Bouzroud et al. (2020); Karlsson et al. (2024)

Note. Limitations are described as tendencies across the corpus; individual studies vary, and the studies cited under mitigation are those that demonstrate the mitigation is achievable rather than those exhibiting the limitation

7. Climate-Amplified Biotic Stress and Susceptibility-Gene Editing

Warming alters pathogen distribution, overwintering, generation number and epidemic timing, so that cultivars selected for resistance under historical conditions face altered pressure, and emerging and re-emerging diseases of fruit and vegetable crops are being reported in association with changing climate (Miller et al., 2024). Disease resistance is therefore part of climate resilience rather than a separate objective, and it is the area in which vegetable genome editing has produced its most convincing evidence.

The dominant strategy inactivates host susceptibility genes rather than introducing resistance genes, which suits Cas9 well because loss of function is the required change. Deletion of the *Mildew Locus O* homologue in tomato produced transgene-free plants resistant to powdery mildew within a short breeding interval (Nekrasov et al., 2017). Targeting of *PMR4*, which encodes a callose synthase, reduced powdery mildew susceptibility, although resistance was partial rather than complete, illustrating that susceptibility-gene inactivation does not necessarily deliver the durable immunity sometimes implied (Santillán Martínez et al., 2020). Editing of *eIF4E* in cucumber conferred broad resistance to several potyviruses in non-transgenic plants, an early demonstration that recessive resistance conserved across species can be engineered directly (Chandrasekaran et al., 2016).

The strongest evidence in the entire corpus reviewed here comes from potato. Cas9 mutants of *StDMR6-1* were evaluated in four consecutive years of field trials at a site with a complex *Phytophthora infestans* (Mont.) de Bary population and showed increased late blight resistance without yield penalty or loss of tuber quality; tubers from those trials also showed increased resistance to common scab, the lines showed increased resistance to *Alternaria solani* Sorauer in controlled experiments, and the mutants were less affected than the background cultivar under controlled drought simulation and salinity (Karlsson et al., 2024). Multi-year field replication, explicit assessment of yield and quality costs, and demonstration of effect across several pathogens and two abiotic stresses combine to produce inference far stronger than anything available for the abiotic-stress-specific loci discussed in Section 4. A second potato study reported that editing a susceptibility gene improved *Phytophthora* resistance without a detectable growth penalty (Bi et al., 2024), which is consistent with the proposition that penalties associated with susceptibility-gene loss are gene specific rather than general.

Two cautions apply. Susceptibility-gene resistance is not automatically durable, since pathogen populations may adapt to the loss of a host factor, and none of the studies reviewed extends over the timescale needed to detect erosion. The evidence from *StDMR6-1* that broad-spectrum susceptibility-gene editing also confers some abiotic-stress advantage is intriguing and, if reproduced, would substantially change how resilience targets are prioritised, since it would indicate shared nodes between biotic and abiotic response networks that could be edited once for multiple benefits. That result currently rests on controlled-condition abiotic assays within a single study and should be treated as a hypothesis worth testing rather than an established property.

8. De Novo Domestication and the Wild Germplasm Argument

A structurally different proposal is to edit domestication and improvement loci in stress-adapted wild relatives rather than edit stress loci in cultivars. The argument is that wild species carry resilience traits assembled by natural selection, and that the small number of major-effect loci distinguishing wild from domesticated forms can be edited directly, bypassing the linkage drag that makes introgression slow. Two groups demonstrated the principle in tomato, editing loci controlling plant architecture, flower and fruit number, fruit size, shape and nutrient content in wild backgrounds to produce plants combining wild genomes with cultivated phenotypes (T. Li et al., 2018; Zsögön et al., 2018). The approach was extended to the orphan Solanaceous species *Physalis pruinosa* L., where editing of orthologues of tomato domestication genes improved plant architecture and fruit size within a single generation (Lemmon et al., 2018), and to the design of compact, early-yielding ideotypes for space-limited production systems (Kwon et al., 2020).

The technical achievement is not in doubt; the resilience claim is. None of these studies demonstrated that the stress tolerance attributed to the wild donor was retained after domestication-gene editing, and there are mechanistic reasons for caution, because the loci edited affect architecture, flowering time and sink strength, all of which interact with stress response. Critical appraisals of the approach make related points, noting that domestication is a population-level process involving many loci and that recreating it by editing a handful of major-effect genes may reproduce the phenotype without the underlying genetic architecture, and drawing attention to the social and intellectual-property questions raised by appropriating wild germplasm in this way (Bartlett et al., 2023). A focused assessment within the Solanaceae reaches similar conclusions about the practical obstacles, including transformation capacity in wild species and the number of loci that would actually need modification (Gasparini et al., 2024).

A more conservative version of the same logic is likely to be more productive in the near term. Rather than domesticate a wild species, deleterious variants fixed during domestication can be repaired in existing cultivars, an approach demonstrated by base editing of a floral regulator in tomato to restore ancestral function (Glaus et al., 2025). Analysis of structural variation across tomato genomes shows how much agronomically relevant regulatory variation was lost or disrupted during domestication and improvement, providing a catalogue of candidates for such repair (Alonge et al., 2020). This route retains the elite background that breeders and growers require, has a much shorter path to deployment, and can be evaluated with conventional agronomic trials.

9. Governance, Access and Acceptance

9.1 Regulatory Divergence and Its Consequences for Research Design

Whether an edited vegetable reaches growers depends on jurisdiction more than on trait quality. Comparative analysis across countries and jurisdictions shows substantial divergence in how edited plants are classified, with several major agricultural producers treating products lacking foreign DNA as equivalent to conventionally bred varieties while others apply the full framework developed for transgenic organisms (Entine et al., 2021). The consequences for research and commercialisation are direct and were evident early in the technology's development (Schmidt et al., 2020), and surveys of products approaching market found that the pattern of development follows regulatory permissiveness rather than agronomic need (Menz et al., 2020). Analysis of global regulatory trends confirms continuing divergence alongside partial convergence on the principle that edits achievable by conventional breeding warrant proportionate treatment (Tachikawa & Matsuo, 2024).

The European position has been the most consequential for vegetable breeding because of the size of the market and the concentration of vegetable seed companies within it. Assessment of the path towards a distinct category of new genomic techniques identifies unresolved questions about detection, traceability and the criteria for equivalence to conventional breeding (Bohle et al., 2024), while analysis in the light of natural plant genetic variation questions whether proposed thresholds are scientifically coherent given the mutational load present in conventional varieties (Schulman et al., 2025). Regulatory divergence also has trade consequences, since asynchronous approval creates the possibility of shipments containing material that is unregulated in the exporting country and regulated in the importing one, a problem particularly acute for perishable vegetable trade (Fernández Ríos et al., 2025).

Regulation shapes the evidence base itself, and this connection is rarely made explicit. Field evaluation of edited plants requires authorisation that is straightforward in some jurisdictions and burdensome in others, so the shortage of field data identified in Section 6 is partly a regulatory artefact. Recognising this reframes the problem: encouraging better evidence requires proportionate field-trial authorisation as much as it requires better experimental practice by researchers.

9.2 Intellectual Property, Capacity and Equitable Access

Vegetable production is dominated globally by smallholders in low-income and middle-income countries, precisely where climate exposure is greatest and where breeding capacity is weakest, so the distribution of access matters as much as technical performance. Patent uncertainty in Europe is one dimension, and the interaction between the patent framework and the proposed regulatory

category for new genomic techniques raises unresolved questions about whether edited varieties remain available for further breeding under the breeders' exemption (Jiang et al., 2025). Analyses of African policy landscapes describe substantial recent progress in establishing enabling frameworks alongside continuing constraints in laboratory infrastructure, regulatory capacity and trained personnel (Akinbo et al., 2025), and assessment of genome editing in sub-Saharan Africa identifies climate adaptation as the principal opportunity while noting the same capacity constraints (Amoah et al., 2024).

The technical constraint identified in Section 3.2 compounds the access problem. Editing capability is concentrated in species and genotypes with established transformation systems, which correspond closely to crops of commercial importance in high-income markets. Indigenous and regionally important vegetables, including many African leafy vegetables and locally adapted cucurbits, lack the transformation and regeneration protocols that editing presupposes. Investment in tissue-culture and regeneration capability for these species would therefore have a larger marginal effect on equitable access than further refinement of nuclease reagents, and the tissue-culture-independent delivery approaches discussed earlier would be disproportionately valuable if they proved transferable (Gupta et al., 2025; Hu et al., 2026).

9.3 Public Acceptance as an Empirical Question

Acceptance is frequently invoked as an obstacle and rarely examined as evidence. Systematic review of public perception of new plant breeding techniques finds that attitudes are shaped by perceived benefit, trust in regulators and institutions, and the framing of information, rather than by a fixed disposition against the technology, and that acceptance is higher when a concrete consumer or environmental benefit is identifiable (Paleologo et al., 2024). Research in Japan, where edited foods have been placed on the market under a notification system, indicates that attitudes are differentiated and context dependent rather than uniformly opposed (Yamaguchi et al., 2024).

The commercial history bears on this. The first edited food products to reach consumers included a tomato with elevated gamma-aminobutyric acid content produced by targeted mutagenesis of the glutamate decarboxylase autoinhibitory domain (Nonaka et al., 2017), and editing work in melon has followed a similar trajectory towards traits with visible consumer or supply-chain benefit (Nonaka & Ezura, 2024; Sasaki et al., 2025). Climate-resilience traits are less visible to consumers than quality traits, which suggests that acceptance strategies developed around quality-trait products will not transfer automatically, and that the benefit case for resilience traits will need to be made in terms of price stability, supply reliability and reduced input use rather than direct product attributes.

10. Future Directions

The priorities set out below follow from the appraisal rather than from a general sense of what would be desirable, and they are ordered by the expected gain in evidential quality per unit of effort. The immediate priorities require no methodological innovation, only changes in experimental design and reporting; the longer-term priorities require capability that does not yet exist for most vegetable species.

The first immediate priority is to establish the relationship between the physiological proxies that dominate the corpus and marketable yield under stress. The unresolved problem is that tolerance claims rest on an inferential step never validated for any vegetable crop, and current evidence is inadequate because no study has measured both proxy variables and yield across a range of stress intensities in the same material. The appropriate design is a dose-response experiment in which a small number of edited lines and their azygous controls are grown across a graded series of water-deficit or salinity treatments to harvest, with electrolyte leakage, malondialdehyde, hydrogen peroxide, gas exchange and marketable yield recorded on the same plants. Tomato and potato are the appropriate species because both have edited lines available and defined yield endpoints. A validated relationship would allow the large body of existing proxy-based evidence to be interpreted rather than discarded, which is the highest-value outcome available from a single modest experiment.

The second immediate priority is multi-environment field evaluation of the small number of alleles for which controlled-environment evidence is strong. The unresolved problem is that field performance may diverge from controlled-environment performance in either direction, and existing evidence is inadequate because only two studies in this corpus report multi-environment or multi-year field data (Karlsson et al., 2024; Lou et al., 2025). The appropriate design is replicated trials at three or more sites spanning the relevant climatic gradient over at least two seasons, with marketable yield, quality and stability across environments as the primary endpoints and with cultivar as an explicit factor. Regulatory authorisation is the binding constraint rather than technical capability, which makes proportionate field-trial permitting a research-policy priority in its own right.

The third immediate priority is to test the combined-stress hypothesis raised by the *SlMAPK3* results. The unresolved problem is that the same allele appears beneficial under one stress and detrimental under another, and evidence is inadequate because no study has imposed the stresses in combination on the same lines. The appropriate design is a factorial experiment applying heat, water deficit and their combination to existing mutant lines and near-isogenic controls at the reproductive stage, with pollen viability, fruit set and yield as endpoints. The outcome would determine whether stress-specific alleles are usable at all in field environments where stresses co-occur, which is a precondition for any deployment strategy built on them.

The fourth priority, on a medium timescale, is to shift from knockout to regulatory engineering for quantitative resilience traits. The unresolved problem is that loss of function accesses only one extreme of the phenotypic range and is frequently the wrong direction of change, as the *SlCBF1* and *SlNPR1* results demonstrate (R. Li et al., 2018, 2019). Evidence that regulatory engineering can do better exists but is confined to a single field-validated example (Lou et al., 2025) supported by proof of principle for allelic series

and for functional separation of pleiotropic effects (Hendelman et al., 2021; Rodríguez-Leal et al., 2017). The appropriate approach is to identify physiological bottlenecks that limit yield under stress, as source-sink limitation does under heat, and to install defined regulatory elements that respond conditionally to the stress, rather than to select stress-responsive regulators and remove them. Prime editing and promoter replacement provide the necessary precision (Nobusawa et al., 2026; Vu et al., 2024), and salinity, for which no field-evaluated edited allele exists in any vegetable crop, is the most obvious target.

The fifth priority, on a longer timescale, is to extend editing capability beyond the small set of transformation-competent genotypes. The unresolved problem is that most published vegetable edits exist in genotypes that are not grown commercially, and that many climatically important vegetable species have no functioning transformation protocol at all. Morphogenic regulators, *de novo* meristem induction, protoplast regeneration and tissue-culture-independent delivery each address part of the problem but have been demonstrated principally outside the vegetable groups considered here (Debernardi et al., 2020; Hu et al., 2026; Liu et al., 2022; Maher et al., 2020). Systematic testing of these methods across a defined panel of vegetable species and genotypes, with transformation efficiency and regeneration frequency as reported outcomes, would establish which approaches transfer and would have particular value for regionally important species that current capacity ignores (Akinbo et al., 2025).

The sixth priority is to test whether the apparent abiotic benefit of broad-spectrum susceptibility-gene editing is general. The unresolved problem is that a single study reports reduced sensitivity to drought and salinity alongside multi-pathogen resistance in the same mutants (Karlsson et al., 2024), which would imply shared regulatory nodes between biotic and abiotic response networks. Evidence is inadequate because the observation rests on controlled-condition assays within one study and one species. The appropriate design is independent replication in additional potato backgrounds and in tomato under both controlled and field conditions, with yield endpoints. Confirmation would substantially reorder resilience-breeding priorities by identifying targets that address several stresses simultaneously.

Table 5 summarises these priorities, stating for each the unresolved problem, the design most likely to resolve it and the outcome measures required. The table separates immediate priorities, which are achievable with existing material and methods, from longer-term priorities that require new capability, and its principal message is that the highest-value work in this field currently involves better evaluation of alleles that already exist rather than the creation of further alleles.

Table 5. Prioritised research needs in genome editing for climate-resilient vegetable crops

Priority and horizon	Unresolved problem	Recommended design	Required outcome measures	Supporting references
Validate proxy-to-yield relationships (immediate)	Tolerance claims rest on damage proxies whose relationship to yield is untested	Dose-response trial across graded stress intensities using existing edited lines and azygous controls, grown to harvest	Damage proxies and marketable yield measured on the same plants across stress levels	R. Li et al. (2019); Tran et al. (2021); Wang et al. (2017)
Multi-environment field evaluation (immediate)	Field performance of promising alleles is largely unknown	Replicated trials at three or more sites over at least two seasons, with cultivar as an explicit factor	Marketable yield, quality and cross-environment stability	Karlsson et al. (2024); Lou et al. (2025)
Combined-stress testing (immediate)	The same allele appears beneficial under one stress and detrimental under another	Factorial imposition of heat, water deficit and their combination on existing mutant lines at the reproductive stage	Pollen viability, fruit set and yield under single and combined stress	Wang et al. (2017); Yu et al. (2019)
Shift to conditional regulatory engineering (medium term)	Knockout accesses only one extreme of the phenotypic range and is often the wrong direction of change	Install stress-responsive regulatory elements at physiological bottleneck loci in elite backgrounds using prime editing or promoter replacement	Stress-responsive expression, carbon partitioning and yield under stress and non-stress conditions	Lou et al. (2025); Nobusawa et al. (2026); Rodríguez-Leal et al. (2017); Vu et al. (2024)
Extend editing beyond transformation-competent genotypes (long term)	Most edits exist in genotypes that are not commercially grown, and many vegetable species lack protocols entirely	Systematic comparison of morphogenic regulators, *de novo* meristem induction, protoplast regeneration and viral delivery across a defined species and genotype panel	Transformation efficiency, regeneration frequency and heritability of edits by genotype	Debernardi et al. (2020); Hu et al. (2026); Liu et al. (2022); Maher et al. (2020)
Test generality of biotic-abiotic co-benefit (long term)	A single study reports abiotic tolerance alongside multi-pathogen resistance in susceptibility-gene mutants	Independent replication in additional potato backgrounds and in tomato, under controlled and field conditions	Pathogen resistance, abiotic stress response and yield in the same material	Bi et al. (2024); Karlsson et al. (2024)

Note. Horizons are indicative: immediate priorities can be addressed with material and methods already reported in the literature, whereas longer-term priorities require capability that does not currently exist for most vegetable species

11. Conclusions

The objectives of this review were to characterise the editing modalities available for vegetable crops, to appraise the evidence that edited alleles confer tolerance of climate-related stresses, to analyse directional inconsistency in that evidence, to identify the methodological features limiting inference, and to set out actionable research priorities together with the conditions governing deployment. The appraisal supports a set of conclusions that differ in the confidence they warrant.

The most secure conclusion is that the technical capacity to create defined alleles in several vegetable species is established, and that this capacity now extends beyond gene inactivation to substitution, insertion and the tuning of transcriptional output. The corresponding conclusion about deployment is much weaker. The published evidence that edited alleles improve performance under climate-related abiotic stress in vegetable crops is, with few exceptions, evidence of gene function obtained in non-commercial genotypes under controlled conditions using measures of cellular damage rather than agricultural performance. The frequent characterisation of this body of work as a pipeline of climate-resilient cultivars is not supported by the primary studies, several of which report that editing reduced rather than improved tolerance.

A second firm conclusion is that resilience cannot be treated as a unitary transferable property. The demonstration that knockout of a single kinase improves tolerance of one stress while impairing tolerance of another indicates that alleles are stress specific and that reactive oxygen species signalling has stress-dependent optima. Because field environments impose stresses in combination, this is not an academic qualification but a constraint on whether such alleles can be deployed at all, and it has not been tested experimentally.

A third conclusion, held with moderate confidence, is that the limiting factor in this field is experimental design and delivery capability rather than nuclease performance. The studies that combine allele-resolution editing of regulatory sequence with elite genetic backgrounds, field environments and yield endpoints produce inference of a different quality from the remainder of the corpus, and they do so using methods available to any adequately equipped laboratory. Where such designs have been applied, whether to heat-responsive carbon partitioning or to multi-year field evaluation of susceptibility-gene mutants, the results have been favourable and have included explicit assessment of trade-offs. Their rarity reflects cost, regulatory friction and disciplinary convention rather than technical impossibility.

A fourth conclusion concerns direction of effort. Regulatory and cis-regulatory engineering addresses the quantitative, dosage-dependent character of resilience traits in a way that knockout cannot, and the natural-variation evidence indicating that much agronomically important variation is regulatory reinforces the case. Selecting a physiological bottleneck and installing conditional expression at it is a fundamentally different strategy from selecting a stress-responsive gene and removing it, and the available evidence favours the former.

The broader significance of this synthesis lies in the relationship between evidential standards and deployment. Vegetable crops are climatically exposed, nutritionally important and produced disproportionately by growers with limited access to new varieties, so the cost of overstating readiness is borne unevenly. Regulatory divergence, patent uncertainty and the concentration of transformation capability in a few species and genotypes mean that technical capability alone will not deliver climate-resilient vegetables. Confidence that genome editing will contribute materially to climate adaptation in vegetable production is reasonable on mechanistic and technical grounds; confidence that it has yet done so is not warranted by the present evidence.

12. Limitations

This review is a narrative synthesis and carries the limitations intrinsic to that design. Study selection was purposive and interpretive rather than protocol-driven, so selection bias cannot be excluded despite the transparent reporting of sources, search strings and eligibility rules, and a second reviewer applying the same criteria might have retained a different set of studies. The thematic organisation and the explanations offered for inconsistent findings are interpretations developed during synthesis, and readers may reasonably weigh the same evidence differently. No formal quality-appraisal instrument was applied, because none validated for this literature exists, so appraisal rested on criteria stated in the methods rather than on scored assessment.

Access to literature was incomplete. Subscription-restricted indexes were unavailable, and one open scholarly index could not be queried, so relevant work indexed only in those resources may have been missed; coverage of agricultural and horticultural literature outside the biomedical indexing tradition is a particular concern, since some vegetable-breeding research appears in journals with limited indexing in the sources that were accessible. The restriction to English will have excluded relevant work published in Chinese, Japanese, Korean and Spanish, which is a substantive limitation for a topic in which several leading research programmes are located in East Asia and Latin America.

The evidence base itself constrains what could be concluded. Study designs, stress protocols, developmental stages and endpoints are heterogeneous to a degree that precludes quantitative synthesis, so no effect sizes are reported and no meta-analytic estimate of the benefit of editing for stress tolerance was possible. The corpus is geographically concentrated, with tomato work dominated by a small number of research groups and several key comparisons resting on studies from a single laboratory, which limits independence. Long-term evidence is scarce: only one study reported multi-year field evaluation, and no study addressed durability of resistance or stability of tolerance across many seasons. Comparability among studies is further reduced by the concentration of work in a small number of genetic backgrounds. The field is developing quickly, particularly in prime editing and delivery technology, so conclusions about technical capability may date faster than conclusions about evidential standards.

Declaration of AI Use

This manuscript was prepared through the combined contributions of all author(s), including contributions to the study design, data, content development, results, interpretation, and related scholarly work. The author(s) acknowledge the use of Grammarly and ChatGPT to assist with grammar checking, language refinement, reference formatting. These AI-assisted tools were not used as authors and did not replace the intellectual contributions or scholarly judgment of the author(s). All AI-assisted outputs, including content, references, and interpretations, were carefully reviewed, revised, verified, and approved by the author(s). The author(s) accept full responsibility for the accuracy, integrity, and final content of the manuscript.

Competing Interests

Authors have declared that no competing interests exist.

References

Akinbo, O., Nkhabindze, B., Amedu, J., Ebegba, R., Asagbra, A., Ratemo, B. O., et al. (2025). Africa and zero hunger agenda: Genome editing policy landscape, challenges and opportunities. *Frontiers in Bioengineering and Biotechnology, 13*, 1526851. https://doi.org/10.3389/fbioe.2025.1526851

Alonge, M., Wang, X., Benoit, M., Soyk, S., Pereira, L., Zhang, L., Suresh, H., Ramakrishnan, S., et al. (2020). Major impacts of widespread structural variation on gene expression and crop improvement in tomato. *Cell, 182*(1), 145–161.e23. https://doi.org/10.1016/j.cell.2020.05.021

Amoah, P., Oumarou Mahamane, A.-R., Byiringiro, M. H., Mahula, N. J., Manneh, N., Oluwasegun, Y. R., Assfaw, A. T., Mukiti, H. M., Garba, A. D., Chiemeke, F. K., Bernard Ojuederie, O., & Olasanmi, B. (2024). Genome editing in Sub-Saharan Africa: A game-changing strategy for climate change mitigation and sustainable agriculture. *GM Crops & Food, 15*(1), 279–302. https://doi.org/10.1080/21645698.2024.2411767

Baethge, C., Goldbeck-Wood, S., & Mertens, S. (2019). SANRA—a scale for the quality assessment of narrative review articles. *Research Integrity and Peer Review, 4*, 5. https://doi.org/10.1186/s41073-019-0064-8

Bartlett, M. E., Moyers, B. T., Man, J., Subramaniam, B., & Makunga, N. P. (2023). The power and perils of de novo domestication using genome editing. *Annual Review of Plant Biology, 74*, 727–750. https://doi.org/10.1146/annurev-arplant-053122-030653

Beracochea, V., Stritzler, M., Radonic, L., Bottero, E., Jozefkowicz, C., Darqui, F., Ayub, N., Bilbao, M. L., & Soto, G. (2023). CRISPR/Cas9-mediated knockout of SPL13 radically increases lettuce yield. *Plant Cell Reports, 42*(3), 645–647. https://doi.org/10.1007/s00299-022-02952-0

Bertier, L. D., Ron, M., Huo, H., Bradford, K. J., Britt, A. B., & Michelmore, R. W. (2018). High-resolution analysis of the efficiency, heritability, and editing outcomes of CRISPR/Cas9-induced modifications of NCED4 in lettuce (*Lactuca sativa*). *G3: Genes, Genomes, Genetics, 8*(5), 1513–1521. https://doi.org/10.1534/g3.117.300396

Bi, W., Liu, J., Li, Y., He, Z., Chen, Y., Zhao, T., Liang, X., Wang, X., Meng, X., Dou, D., & Xu, G. (2024). CRISPR/Cas9-guided editing of a novel susceptibility gene in potato improves *Phytophthora* resistance without growth penalty. *Plant Biotechnology Journal, 22*(1), 4–6. https://doi.org/10.1111/pbi.14175

Bineau, E., Diouf, I., Carretero, Y., Duboscq, R., Bitton, F., Djari, A., Zouine, M., & Causse, M. (2021). Genetic diversity of tomato response to heat stress at the QTL and transcriptome levels. *The Plant Journal, 107*(4), 1213–1227. https://doi.org/10.1111/tpj.15379

Bisbis, M. B., Gruda, N., & Blanke, M. (2018). Potential impacts of climate change on vegetable production and product quality: A review. *Journal of Cleaner Production, 170*, 1602–1620. https://doi.org/10.1016/j.jclepro.2017.09.224

Bohle, F., Schneider, R., Mundorf, J., Zühl, L., Simon, S., & Engelhard, M. (2024). Where does the EU-path on new genomic techniques lead us? *Frontiers in Genome Editing, 6*, 1377117. https://doi.org/10.3389/fgeed.2024.1377117

Bouzroud, S., Gasparini, K., Hu, G., Barbosa, M. A. M., Rosa, B. L., Fahr, M., Bendaou, N., Bouzayen, M., Zsögön, A., Smouni, A., & Zouine, M. (2020). Down regulation and loss of auxin response factor 4 function using CRISPR/Cas9 alters plant growth, stomatal function and improves tomato tolerance to salinity and osmotic stress. *Genes, 11*(3), 272. https://doi.org/10.3390/genes11030272

Chandrasekaran, J., Brumin, M., Wolf, D., Leibman, D., Klap, C., Pearlsman, M., Sherman, A., Arazi, T., & Gal-On, A. (2016). Development of broad virus resistance in non-transgenic cucumber using CRISPR/Cas9 technology. *Molecular Plant Pathology, 17*(7), 1140–1153. https://doi.org/10.1111/mpp.12375

Choi, S. H., Ahn, W. S., Jie, E. Y., Cho, H.-S., & Kim, S. W. (2022). Development of late-bolting plants by CRISPR/Cas9-mediated genome editing from mesophyll protoplasts of lettuce. *Plant Cell Reports, 41*(7), 1627–1630. https://doi.org/10.1007/s00299-022-02875-w

Das, T., Anand, U., Pal, T., Mandal, S., Kumar, M., Radha, Gopalakrishnan, A. V., Pérez de la Lastra, J. M., & Dey, A. (2023). Exploring the potential of CRISPR/Cas genome editing for vegetable crop improvement: An overview of challenges and approaches. *Biotechnology and Bioengineering, 120*(5), 1215–1228. https://doi.org/10.1002/bit.28344

Debernardi, J. M., Tricoli, D. M., Ercoli, M. F., Hayta, S., Ronald, P., Palatnik, J. F., & Dubcovsky, J. (2020). A GRF–GIF chimeric protein improves the regeneration efficiency of transgenic plants. *Nature Biotechnology, 38*(11), 1274–1279. https://doi.org/10.1038/s41587-020-0703-0

Decima Oneto, C. A., Massa, G. A., Echarte, L., Rey Burusco, M. F., Gonzalez, M. N., Alfonso, C. S., Laserna, M. P., Norero, N. S., Divito, S. B., & Feingold, S. E. (2025). CRISPR/Cas9 editing of CBP80 enhances drought tolerance in potato (*Solanum tuberosum*). *Frontiers in Plant Science, 16*, 1598947. https://doi.org/10.3389/fpls.2025.1598947

Devi, R., Chauhan, S., & Dhillon, T. S. (2022). Genome editing for vegetable crop improvement: Challenges and future prospects. *Frontiers in Genetics, 13*, 1037091. https://doi.org/10.3389/fgene.2022.1037091

Entine, J., Felipe, M. S. S., Groenewald, J.-H., Kershen, D. L., Lema, M., McHughen, A., Nepomuceno, A. L., Ohsawa, R., et al. (2021). Regulatory approaches for genome edited agricultural plants in select countries and jurisdictions around the world. *Transgenic Research, 30*(4), 551–584. https://doi.org/10.1007/s11248-021-00257-8

Fernández Ríos, D., Quintana, S. A., Gómez Paniagua, P., Arrúa, A. A., Brozón, G. R., Bertoni Hicar, M. S., Castro Alegría, A., & Goberna, M. F. (2025). Regulatory challenges and global trade implications of genome editing in agriculture. *Frontiers in Bioengineering and Biotechnology, 13*, 1609110. https://doi.org/10.3389/fbioe.2025.1609110

Gasparini, K., Figueiredo, Y. G., Araújo, W. L., Peres, L. E. P., & Zsögön, A. (2024). De novo domestication in the Solanaceae: Advances and challenges. *Current Opinion in Biotechnology, 89*, 103177. https://doi.org/10.1016/j.copbio.2024.103177

Glaus, A. N., Brechet, M., Swinnen, G., Lebeigle, L., Iwaszkiewicz, J., Ambrosini, G., Julca, I., Zhang, J., Roberts, R., Iseli, C., Guex, N., Jiménez-Gómez, J., Glover, N., Martin, G. B., Strickler, S., & Soyk, S. (2025). Repairing a deleterious domestication variant in a floral regulator gene of tomato by base editing. *Nature Genetics, 57*(1), 231–241. https://doi.org/10.1038/s41588-024-02026-9

Graham, N., Patil, G. B., Bubeck, D. M., Dobert, R. C., Glenn, K. C., Gutsche, A. T., Kumar, S., Lindbo, J. A., et al. (2020). Plant genome editing and the relevance of off-target changes. *Plant Physiology, 183*(4), 1453–1471. https://doi.org/10.1104/pp.19.01194

Grant, M. J., & Booth, A. (2009). A typology of reviews: An analysis of 14 review types and associated methodologies. *Health Information & Libraries Journal, 26*(2), 91–108. https://doi.org/10.1111/j.1471-1842.2009.00848.x

Greenhalgh, T., Thorne, S., & Malterud, K. (2018). Time to challenge the spurious hierarchy of systematic over narrative reviews? *European Journal of Clinical Investigation, 48*(6), e12931. https://doi.org/10.1111/eci.12931

Gupta, I., Sharma, J. G., & Kaul, T. (2025). Nanoparticle-driven CRISPR-Cas9 genome editing: A new frontier in crop improvement. *Molecular Biology Reports, 52*(1), 1015. https://doi.org/10.1007/s11033-025-11064-3

Hendelman, A., Zebell, S., Rodriguez-Leal, D., Dukler, N., Robitaille, G., Wu, X., Kostyun, J., Tal, L., Wang, P., Bartlett, M. E., Eshed, Y., Efroni, I., & Lippman, Z. B. (2021). Conserved pleiotropy of an ancient plant homeobox gene uncovered by cis-regulatory dissection. *Cell, 184*(7), 1724–1739.e16. https://doi.org/10.1016/j.cell.2021.02.001

Hu, M., Zhang, L., Herrera-Estrella, L., & Liu, D. (2026). Heritable, tissue culture-independent and transgene-free genome editing in plants via viral delivery of CRISPR/AsCas12f. *Plant Biotechnology Journal, 24*(1), 84–86. https://doi.org/10.1111/pbi.70315

Jiang, L., Adcock, M., & Yang, H. (2025). To patent or not to patent: Challenges and solutions to the patent ban on new genomic techniques plant in EU. *GM Crops & Food, 16*(1), 562–574. https://doi.org/10.1080/21645698.2025.2548638

Karlsson, M., Kieu, N. P., Lenman, M., Marttila, S., Resjö, S., Zahid, M. A., & Andreasson, E. (2024). CRISPR/Cas9 genome editing of potato StDMR6-1 results in plants less affected by different stress conditions. *Horticulture Research, 11*(7), uhae130. https://doi.org/10.1093/hr/uhae130

Kim, Y.-C., Kang, Y., Yang, E.-Y., Cho, M.-C., Schafleitner, R., Lee, J. H., & Jang, S. (2021). Applications and major achievements of genome editing in vegetable crops: A review. *Frontiers in Plant Science, 12*, 688980. https://doi.org/10.3389/fpls.2021.688980

Klap, C., Yeshayahou, E., Bolger, A. M., Arazi, T., Gupta, S. K., Shabtai, S., Usadel, B., Salts, Y., & Barg, R. (2017). Tomato facultative parthenocarpy results from SlAGAMOUS-LIKE 6 loss of function. *Plant Biotechnology Journal, 15*(5), 634–647. https://doi.org/10.1111/pbi.12662

Kwon, C.-T., Heo, J., Lemmon, Z. H., Capua, Y., Hutton, S. F., Van Eck, J., Park, S. J., & Lippman, Z. B. (2020). Rapid customization of Solanaceae fruit crops for urban agriculture. *Nature Biotechnology, 38*(2), 182–188. https://doi.org/10.1038/s41587-019-0361-2

Lawrenson, T., Shorinola, O., Stacey, N., Li, C., Østergaard, L., Patron, N., Uauy, C., & Harwood, W. (2015). Induction of targeted, heritable mutations in barley and *Brassica oleracea* using RNA-guided Cas9 nuclease. *Genome Biology, 16*, 258. https://doi.org/10.1186/s13059-015-0826-7

Lee, E., Kim, Y., Kim, M., Lee, D., & Kang, B.-C. (2025). DNA-free base editing in lettuce via in vitro transcribed base editors. *Journal of Integrative Plant Biology, 67*(2), 199–201. https://doi.org/10.1111/jipb.13822

Lemmon, Z. H., Reem, N. T., Dalrymple, J., Soyk, S., Swartwood, K. E., Rodriguez-Leal, D., Van Eck, J., & Lippman, Z. B. (2018). Rapid improvement of domestication traits in an orphan crop by genome editing. *Nature Plants, 4*(10), 766–770. https://doi.org/10.1038/s41477-018-0259-x

Li, R., Liu, C., Zhao, R., Wang, L., Chen, L., Yu, W., Zhang, S., Sheng, J., & Shen, L. (2019). CRISPR/Cas9-mediated SlNPR1 mutagenesis reduces tomato plant drought tolerance. *BMC Plant Biology, 19*, 38. https://doi.org/10.1186/s12870-018-1627-4

Li, R., Zhang, L., Wang, L., Chen, L., Zhao, R., Sheng, J., & Shen, L. (2018). Reduction of tomato-plant chilling tolerance by CRISPR–Cas9-mediated SlCBF1 mutagenesis. *Journal of Agricultural and Food Chemistry, 66*(34), 9042–9051. https://doi.org/10.1021/acs.jafc.8b02177

Li, T., Yang, X., Yu, Y., Si, X., Zhai, X., Zhang, H., Dong, W., Gao, C., & Xu, C. (2018). Domestication of wild tomato is accelerated by genome editing. *Nature Biotechnology, 36*(12), 1160–1163. https://doi.org/10.1038/nbt.4273

Li, Y., Zhang, X., Xia, C., Wu, T., Gao, Y., Zeng, L., Wu, Z., Dai, X., Yuan, F., Liu, F., Yang, S., & Zou, X. (2026). Molecular mechanisms and breeding strategies for heat tolerance in vegetable crops under global warming. *Horticulture Research, 13*(2), uhaf309. https://doi.org/10.1093/hr/uhaf309

Liu, Y., Andersson, M., Granell, A., Cardi, T., Hofvander, P., & Nicolia, A. (2022). Establishment of a DNA-free genome editing and protoplast regeneration method in cultivated tomato (*Solanum lycopersicum*). *Plant Cell Reports, 41*(9), 1843–1852. https://doi.org/10.1007/s00299-022-02893-8

Lou, H., Li, S., Shi, Z., Zou, Y., Zhang, Y., Huang, X., Yang, D., Yang, Y., Li, Z., & Xu, C. (2025). Engineering source-sink relations by prime editing confers heat-stress resilience in tomato and rice. *Cell, 188*(2), 530–549.e20. https://doi.org/10.1016/j.cell.2024.11.005

Maher, M. F., Nasti, R. A., Vollbrecht, M., Starker, C. G., Clark, M. D., & Voytas, D. F. (2020). Plant gene editing through de novo induction of meristems. *Nature Biotechnology, 38*(1), 84–89. https://doi.org/10.1038/s41587-019-0337-2

Menz, J., Modrzejewski, D., Hartung, F., Wilhelm, R., & Sprink, T. (2020). Genome edited crops touch the market: A view on the global development and regulatory environment. *Frontiers in Plant Science, 11*, 586027. https://doi.org/10.3389/fpls.2020.586027

Miller, S. A., Testen, A. L., Jacobs, J. M., & Lewis Ivey, M. L. (2024). Mitigating emerging and reemerging diseases of fruit and vegetable crops in a changing climate. *Phytopathology, 114*(5), 917–929. https://doi.org/10.1094/PHYTO-10-23-0393-KC

Nekrasov, V., Wang, C., Win, J., Lanz, C., Weigel, D., & Kamoun, S. (2017). Rapid generation of a transgene-free powdery mildew resistant tomato by genome deletion. *Scientific Reports, 7*, 482. https://doi.org/10.1038/s41598-017-00578-x

Nobusawa, T., Yamatani, H., & Kusaba, M. (2026). Promoter/enhancer replacement by genome editing for crop improvement. *Trends in Plant Science, 31*(3), 273–281. https://doi.org/10.1016/j.tplants.2025.10.016

Nonaka, S., & Ezura, H. (2024). Possibility of genome editing for melon breeding. *Breeding Science, 74*(1), 47–58. https://doi.org/10.1270/jsbbs.23074

Nonaka, S., Arai, C., Takayama, M., Matsukura, C., & Ezura, H. (2017). Efficient increase of γ-aminobutyric acid (GABA) content in tomato fruits by targeted mutagenesis. *Scientific Reports, 7*, 7057. https://doi.org/10.1038/s41598-017-06400-y

Paleologo, M., Lanubile, A., Camardo Leggieri, M., Graffigna, G., Gomarasca, P., & Barello, S. (2024). Public perception of new plant breeding techniques and the psychosocial determinants of acceptance: A systematic review. *Public Understanding of Science, 33*(6), 795–812. https://doi.org/10.1177/09636625241254981

Postiglione, A. E., Delange, A. M., Ali, M. F., Wang, E. Y., Houben, M., Hahn, S. L., Khoury, M. G., Roark, C. M., Davis, M., Reid, R. W., Pease, J. B., Loraine, A. E., & Muday, G. K. (2024). Flavonols improve tomato pollen thermotolerance during germination and tube elongation by maintaining reactive oxygen species homeostasis. *The Plant Cell, 36*(10), 4511–4534. https://doi.org/10.1093/plcell/koae222

Rodríguez-Leal, D., Lemmon, Z. H., Man, J., Bartlett, M. E., & Lippman, Z. B. (2017). Engineering quantitative trait variation for crop improvement by genome editing. *Cell, 171*(2), 470–480.e8. https://doi.org/10.1016/j.cell.2017.08.030

Santillán Martínez, M. I., Bracuto, V., Koseoglou, E., Appiano, M., Jacobsen, E., Visser, R. G. F., Wolters, A.-M. A., & Bai, Y. (2020). CRISPR/Cas9-targeted mutagenesis of the tomato susceptibility gene PMR4 for resistance against powdery mildew. *BMC Plant Biology, 20*, 284. https://doi.org/10.1186/s12870-020-02497-y

Sasaki, K., Urano, K., Mimida, N., Nonaka, S., Ezura, H., & Imai, R. (2025). A long shelf-life melon created via CRISPR/Cas9 RNP-based in planta genome editing. *Frontiers in Genome Editing, 7*, 1623097. https://doi.org/10.3389/fgeed.2025.1623097

Scheelbeek, P. F. D., Bird, F. A., Tuomisto, H. L., Green, R., Harris, F. B., Joy, E. J. M., Chalabi, Z., Allen, E., Haines, A., & Dangour, A. D. (2018). Effect of environmental changes on vegetable and legume yields and nutritional quality. *Proceedings of the National Academy of Sciences, 115*(26), 6804–6809. https://doi.org/10.1073/pnas.1800442115

Schmidt, S. M., Belisle, M., & Frommer, W. B. (2020). The evolving landscape around genome editing in agriculture. *EMBO Reports, 21*(6), e50680. https://doi.org/10.15252/embr.202050680

Schulman, A. H., Hartung, F., Smulders, M. J. M., Sundström, J. F., Wilhelm, R., Rognli, O. A., & Metzlaff, K. (2025). Proposed EU NGT legislation in light of plant genetic variation. *Plant Biotechnology Journal, 23*(10), 4261–4270. https://doi.org/10.1111/pbi.70228

Shelake, R. M., Kadam, U. S., Kumar, R., Pramanik, D., Singh, A. K., & Kim, J.-Y. (2022). Engineering drought and salinity tolerance traits in crops through CRISPR-mediated genome editing: Targets, tools, challenges, and perspectives. *Plant Communications, 3*(6), 100417. https://doi.org/10.1016/j.xplc.2022.100417

Sood, A., Sharma, P., Sharma, A., Chaudhary, D. R., & Manisha. (2025). Genome editing in vegetable crops: A new era of sustainable agriculture. *Molecular Biology Reports, 52*(1), 944. https://doi.org/10.1007/s11033-025-11063-4

Sukhera, J. (2022). Narrative reviews: Flexible, rigorous, and practical. *Journal of Graduate Medical Education, 14*(4), 414–417. https://doi.org/10.4300/JGME-D-22-00480.1

Swinnen, G., Lizé, E., Loera Sánchez, M., Stolz, S., & Soyk, S. (2025). Application of a GRF-GIF chimera enhances plant regeneration for genome editing in tomato. *Plant Biotechnology Journal, 23*(9), 4044–4056. https://doi.org/10.1111/pbi.70212

Tachikawa, M., & Matsuo, M. (2024). Global regulatory trends of genome editing technology in agriculture and food. *Breeding Science, 74*(1), 3–10. https://doi.org/10.1270/jsbbs.23046

Tang, X., Liu, G., Zhou, J., Ren, Q., You, Q., Tian, L., Xin, X., Zhong, Z., Liu, B., Zheng, X., Zhang, D., Malzahn, A., Gong, Z., Qi, Y., Zhang, T., & Zhang, Y. (2018). A large-scale whole-genome sequencing analysis reveals highly specific genome editing by both Cas9 and Cpf1 (Cas12a) nucleases in rice. *Genome Biology, 19*, 84. https://doi.org/10.1186/s13059-018-1458-5

Ton, L. B., Qayyum, Z., Amas, J., Thomas, W. J. W., Edwards, D., Batley, J., & Dolatabadian, A. (2025). Applications of CRISPR/Cas tools in improving stress tolerance in *Brassica* crops. *Frontiers in Plant Science, 16*, 1616526. https://doi.org/10.3389/fpls.2025.1616526

Tran, M. T., Doan, D. T. H., Kim, J., Song, Y. J., Sung, Y. W., Das, S., Kim, E.-J., Son, G. H., Kim, S. H., Van Vu, T., & Kim, J.-Y. (2021). CRISPR/Cas9-based precise excision of SlHyPRP1 domain(s) to obtain salt stress-tolerant tomato. *Plant Cell Reports, 40*(6), 999–1011. https://doi.org/10.1007/s00299-020-02622-z

Tuncel, A., Pan, C., Clem, J. S., Liu, D., & Qi, Y. (2025). CRISPR–Cas applications in agriculture and plant research. *Nature Reviews Molecular Cell Biology, 26*, 419–441. https://doi.org/10.1038/s41580-025-00834-3

Veillet, F., Perrot, L., Chauvin, L., Kermarrec, M.-P., Guyon-Debast, A., Chauvin, J.-E., Nogué, F., & Mazier, M. (2019). Transgene-free genome editing in tomato and potato plants using *Agrobacterium*-mediated delivery of a CRISPR/Cas9 cytidine base editor. *International Journal of Molecular Sciences, 20*(2), 402. https://doi.org/10.3390/ijms20020402

Vu, T. V., Nguyen, N. T., Kim, J., Song, Y. J., Nguyen, T. H., & Kim, J.-Y. (2024). Optimized dicot prime editing enables heritable desired edits in tomato and *Arabidopsis*. *Nature Plants, 10*(10), 1502–1513. https://doi.org/10.1038/s41477-024-01786-w

Wang, L., Chen, L., Li, R., Zhao, R., Yang, M., Sheng, J., & Shen, L. (2017). Reduced drought tolerance by CRISPR/Cas9-mediated SlMAPK3 mutagenesis in tomato plants. *Journal of Agricultural and Food Chemistry, 65*(39), 8674–8682. https://doi.org/10.1021/acs.jafc.7b02745

Wen, J., Jiang, F., Weng, Y., Sun, M., Shi, X., Zhou, Y., Yu, L., & Wu, Z. (2019). Identification of heat-tolerance QTLs and high-temperature stress-responsive genes through conventional QTL mapping, QTL-seq and RNA-seq in tomato. *BMC Plant Biology, 19*, 398. https://doi.org/10.1186/s12870-019-2008-3

Wu, W., Wang, R., Li, J., Zhang, Z., Yao, W., Zhang, N., & Xu, W. (2026). Engineering climate-resilient horticultural crops: Advances in transcriptional regulation, genome editing, and synthetic networks. *Horticulture Research, 13*(8), uhag119. https://doi.org/10.1093/hr/uhag119

Xie, D.-L., Huang, H.-M., Zhou, C.-Y., Liu, C.-X., Kanwar, M. K., Qi, Z.-Y., & Zhou, J. (2022). HsfA1a confers pollen thermotolerance through upregulating antioxidant capacity, protein repair, and degradation in *Solanum lycopersicum* L. *Horticulture Research, 9*, uhac163. https://doi.org/10.1093/hr/uhac163

Yamaguchi, T., Ezaki, K., & Ito, K. (2024). Exploring the landscape of public attitudes towards gene-edited foods in Japan. *Breeding Science, 74*(1), 11–21. https://doi.org/10.1270/jsbbs.23047

Yu, W., Wang, L., Zhao, R., Sheng, J., Zhang, S., Li, R., & Shen, L. (2019). Knockout of SlMAPK3 enhances tolerance to heat stress involving ROS homeostasis in tomato plants. *BMC Plant Biology, 19*, 354. https://doi.org/10.1186/s12870-019-1939-z

Zsögön, A., Čermák, T., Naves, E. R., Notini, M. M., Edel, K. H., Weinl, S., Freschi, L., Voytas, D. F., Kudla, J., & Peres, L. E. P. (2018). De novo domestication of wild tomato using genome editing. *Nature Biotechnology, 36*(12), 1211–1216. https://doi.org/10.1038/nbt.4272

Peer-review history:
The peer review history for this paper can be accessed here:
https://pr.sdiarticle5.com/review-history/164528